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THE FUSARIUM YELLOWS DISEASE OF CELERY

(*Apium Graveolens L. Var. Dulce D. C.*)

RAY NELSON, G. H. COONS AND L. C. COCHRAN

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AGRICULTURAL EXPERIMENT STATION
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The Fusarium Yellows Disease of Celery

(*Apium Graveolens L. Var. Dulce D. C.*)[1]

RAY NELSON, G. H. COONS[2], AND L. C. COCHRAN[3]

Celery is one of the most important truck crops and its value per acre is seldom exceeded by other vegetables and small fruits. Its high rank as a cash crop is shown by a comparison with a few of the other widely grown truck crops. In 1934 the farm value of celery per acre was approximately double that of either lettuce, onions or asparagus, quadruple that of beans or cantaloupes, and five times that of cabbage (53)[4]. Despite a small acreage as compared with other truck crops, celery had a farm value in 1934 exceeded only by tomatoes, peas, lettuce, strawberries, and potatoes.

In Michigan the commercial production of celery has increased steadily since the inception of the industry. In 1919 approximately 2,500 acres were grown with a total farm value of $435,000. By 1931 the acreage, chiefly by expansion of new areas, had increased to 7,290 with a farm value of $2,570,000. Previously, Michigan ranked third or fourth in acreage planted, but in 1934 and 1935 only California had more extensive plantings.

The Michigan celery industry is concentrated mostly in Kalamazoo, Muskegon, Allegan, Ottawa, Kent, and Van Buren counties, with scattered areas in other counties producing celery for local sale. Different systems of culture are employed which differentiate the producing sections into the so-called summer celery and winter celery districts. In Kalamazoo County, especially, and to a less extent in Muskegon and Ottawa counties, an intensive and continuous culture, which includes two and three plantings on the same field each season, is practiced. This continuous cropping of the land with celery is especially conducive to the development of disease. At Kalamazoo there are many fields of muck soil on which successive crops of celery have been grown for more than 65 years (19). Under such conditions of intensive culture, the root parasites have become a much more serious menace than in sections where crop rotation can operate as a sanitation measure. The Fusarium yellows disease, with the chief center of infestation at Kalamazoo, has been a constant menace to the Michigan celery

[1]The writers are indebted to Dr. E. A. Bessey for helpful suggestions and for aid in the preparation of the manuscript. They also acknowledge the cooperation of various Kalamazoo celery growers, especially Mr. John Kline, president of Kalamazoo Celery Growers' Improvement League, which has expedited the field work of these investigations. They are especially obligated to Dr. I. C. Jagger, U. S. Dept. of Agr., Chula Vista, Calif., who has supervised the growing and production of the seed stock of the resistant varieties of celery and who has given material assistance in that phase of the problem.

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[4]The numbers in parentheses refer to literature cited, page 72.

industry for at least 25 years. The potential destructiveness of this disease and the great importance of the industry, were responsible for the initiation of the investigational work which has been carried on almost uninterruptedly for two decades. The results of these researches are presented in this paper.

HISTORY OF THE DISEASE IN MICHIGAN

The early history of Fusarium yellows is of interest in showing the seriousness of the disease and its rate of spread—not only in the Kalamazoo area but throughout the other celery districts. The history, therefore, is given in some detail.

During the summer of 1913 the county agricultural agent at Kalamazoo called to the attention of the Michigan Agricultural Experiment Station a serious disease of celery which was prevalent in the marshes about that city and which was the cause of grave concern among the growers. Its distribution in those areas and the complete destruction of some plantings indicated that the disease had been present for several years previously.

In 1914 a survey was made of celery fields in the Kalamazoo area, and the distribution and the general importance of the disease was determined. Many plantings were generally affected, while others showed the effects of the disease only in restricted areas. Infected plants were seen at Portage, one of the contiguous sections in Kalamazoo county, and during 1914 and 1915 diseased plants were found in the important producing sections of Decatur, Grand Haven, and Zeeland.

By 1918 the range of the disease had been extended considerably at Kalamazoo. A re-survey of this district and of the contiguous ones of Comstock and Portage showed that the infested area was greatly enlarged over that mapped in 1914 (Pl. 8). In the south marsh section of Kalamazoo, many fields that in 1914 had shown only localized areas where affected plants occurred, were now almost totally infested. In June 1916, the creek which drains the marshes overflowed its bank and flooded many fields. Infested soil was deposited over a wide area, including fields on which no diseased plants had previously been found. Consequently, the area of infection was greatly extended, and the disease developed so generally in the fields of this district that plans which had been made to attempt eradication by steaming the affected parts of fields had to be abandoned. In this same season yellows was first found in Jackson and Bay counties. In a series of brief progress reports, Coons described the disease and outlined some of the various phases of investigation which were initiated (3, 4, 5, 6, 7, 8); further developments were later reported by Coons and Nelson (11, 12, 13).

The spread of yellows to the outlying marshes in Kalamazoo County and to all of the producing sections in Michigan has continued unabated since the discovery of this trouble in 1913. It now occurs in all of the important celery sections of the state, and year by year its range has increased and soil infestation has been intensified. Most of the dissemination in Michigan and the spread into other states has occurred through the medium of infected plants. For a number of years after yellows was discovered, many millions of seedling plants were grown in Kalamazoo County and sold locally, as well as shipped to other Michigan sections and into other states. In many instances an outbreak of disease in a locality previously free of this trouble could be traced to the importation of plants from an infested section. Some of the newer Michigan sections have become seriously infested

in this way, and the recent development of yellows in the Hamilton district probably can be attributed to the use of seedlings imported from other sections in 1933 and 1934 when drouths were responsible for seed bed failures. This important section was the only major celery producing district in Michigan in which yellows had not caused serious damage in previous years.

NAMES AND DISTRIBUTION OF THE DISEASE

Because of the conspicuously dwarfed condition of infected plants, Coons (3), in the first published account of the Fusarium yellows disease in Michigan, suggested that it be called the "stunting disease of celery". Various other terms have been in use to describe the disease. The Kalamazoo growers have always called it "sickness" or "root rot". After the cause of the disease had been determined, the terminology used in connection with similar diseases of other plants was applied to this trouble. The characteristic appearance of diseased plants in the field is well-described by the term "yellows," which previously had been applied to a fusarial disease in cabbage. Since wilting occurs only in late stages of the disease, while a blanching of the foliage is usually a constant symptom in infected plants, the name "yellows" seemed more appropriate than "wilt", and was proposed and used (11) without confusion for a number of years. A disease of celery in California caused by an undescribed strain of the aster yellows virus was reported and named "celery yellows" by Severin (41). As a result of this confusing terminology, the two diseases have not always been distinguished in published reports of their occurrence. To prevent further confusion, it is suggested that the fungous disease be designated as "Fusarium yellows." A more suitable name for the other disease would be "virus yellows of celery."

In 1908 Stone (43) described a disease of celery in Massachusetts which he called "crown rot." A more detailed description was given in 1909 (44) and the statement was made that the disease was first observed in 1907. Observations and preliminary investigations indicated that the disease was of bacterial origin. The description of diseased plants agrees fairly well with the appearance of celery plants infected with the Fusarium disease. It is probable that crown rot as described by Stone was identical with the Michigan disease.

Gardner (14), who was familiar with the Michigan disease, observed it at Indianapolis and Lafayette, Ind. in 1916 and states that the disease was seen at Goshen, Ind., in the fall of 1914.

Crown rot was reported from New Jersey in 1916 by Krout (20), and in this report he states that the disease had been present for at least 10 years. His description of affected plants and a subsequent statement (21) that the causal organism was a bacterium, or a bacterium and a Fusarium working simultaneously, makes it likely that this disease was identical with Fusarium yellows. Additional reports on the New Jersey disease were made by Poole (35, 36), and his account of varietal reactions is further evidence that the Michigan and New Jersey diseases were similar, if not identical.

The known range of Fusarium yellows was extended in 1921 to include Minnesota (47) and Colorado (48). The same year Thomas (45) reported a root and heart rot of celery from Ohio and stated that a Fusarium was associated with the disease. Thomas' 1924 report (46) and the subsequent history of yellows in Ohio indicate that this root and heart rot was the same disease as the one discussed in this bulletin. The Ohio disease is of

special interest because Wollenweber (59), while he was at Washington in 1911, received some diseased celery plants sent to him from Ohio by Jamieson, and from the rotted roots of these plants he isolated a fungus which was identified as *Fusarium orthoceras* (60, No. 359). In reply to an inquiry, Doctor Wollenweber states that he remembers receiving the plants and isolating the fungus, but no infection tests were made. A culture of the fungus which Wollenweber isolated from the diseased plants in 1911 has recently been obtained[5], and has given only negative results in infection tests. A destructive celery root rot of undetermined cause was reported from Ohio by Van Hook in 1907 (54). The diseased plants illustrated do not resemble those affected with yellows.

Celery yellows was reported (49) from two localities in Pennsylvania in 1922, and a record of its occurrence in Niagara County, New York, the same season was sent to the Plant Disease Survey office (49). North Dakota (50) was included in 1924 among the states reporting the occurrence of the disease. In 1925 the disease was observed for the first time in Canada (18).

Milbrath (24) observed in 1926 a disease which was undoubtedly yellows in fields of celery at Chula Vista, and El Monte, Calif. The senior author saw the disease at both Chula Vista and El Monte, Calif., in September 1929, and in March 1934, plants infected with a vascular-invading species of Fusarium were collected at Venice, Calif. Dr. I. C. Jagger first noted the occurrence of the disease at Venice in the fall of 1933 and reported it to the senior author. The Venice disease is of special interest because it appears to differ from yellows as it occurs elsewhere.

Young reported yellows (64) from two counties in Montana in 1930. White Plume celery plants affected with yellows were received in 1931 from a grower at Green Bay, Wis., and the following season (51) the Plant Disease Survey office received the first reports of the occurrence of the disease in that state.

Celery yellows now occurs in all of the important celery-growing sections of the country with the exception of Florida. The absence of the disease there may, in part, be due to temperature conditions not favorable to its development. In reply to an inquiry about a Fusarium root rot of celery in Florida reported by Rolfs in 1905, Dr. H. A. Edson has supplied the following information, based on a 1905 entry in the files of the Plant Disease Survey office: "He (Rolfs) states that the disease was reported to cause serious loss to young plants in seed beds at Wimauma and Manatee. The earliest report came from Wimauma, Oct. 18, 1905. In some cases the loss was reported to be 100 per cent." From the meager information available it is impossible to draw any conclusions concerning the nature of this disease.

The first report of a Fusarium disease of celery in California has also been supplied by Dr. Edson: "In 1910 a report from California records root rot of celery due to *Fusarium* sp. Estimated loss is said to be immaterial and prevalence very little." A footnote states that the trouble occurs only on heavy ground. A second report from California which would seem more likely to refer to Fusarium yellows was received under date of Nov. 1, 1921, from D. G. Milbrath under the heading "Damping Off", *Fusarium* sp.: "In 1921 plantings a large amount of damping off in the form of wilt due to a species of Fusarium was observed. About 5 per cent of 800 acres in the El Monte district was lost." The subsequent record of the development

[5]International Collection of Fungus Cultures.

of yellows in the El Monte district gives some basis for opinion that the damping off in the 1919 crop may have been a manifestation of Fusarium yellows.

IMPORTANCE

In Michigan, Fusarium yellows ranks next to the leaf blights as a destructive disease of celery. The importance of the disease cannot be judged alone from the crop losses that have been sustained. Estimates of these losses can only approximate the direct losses, for some of the secondary effects of the disease that are more difficult to evaluate are none the less important. Some of these losses come from the decline in the value of land used for celery production, experimentation with unprofitable varieties and a loss of prestige which followed the production of varieties that were not equal in quality to the variety grown before the disease became important.

Although the losses from crop failures constitute only a portion of the direct losses sustained by Michigan celery growers, the amount is large. Crop failures were most serious in 1914, 1916, 1919, 1922, and the 8-year period from 1928 to 1935. Those were seasons characterized by drouth and high temperatures. From crop failures alone in those years, the losses to Kalamazoo growers exceeded $1,500,000. Conservative growers estimated the loss in Kalamazoo County in 1931 at $100,000 and for all Michigan districts at $200,000. These estimates indicate the great importance of Fusarium yellows in seasons favorable for its occurrence. The cumulative losses from yellows in Michigan since it was first observed in 1914 may be conservatively placed at from three to five million dollars.

Fusarium yellows has not been so destructive in other states as in Michigan, but the disease has caused serious loss at various times in Ohio, Indiana, Massachusetts, New Jersey, New York, and Colorado. The history of the disease has been similar to that in Michigan and it has been necessary to use resistant varieties in order to continue the culture of celery in the infested areas. In most of these sections the spread and destructiveness of yellows has been in proportion to the cultural system employed. As a consequence, it is still possible to raise susceptible varieties in some of the sections where a one-crop system is used. Susceptible varieties are rapidly being displaced in areas where a more intensive cropping is followed.

Osmun (34) reported almost complete failure of Golden Self-Blanching from crown rot on some farms in Massachusetts as early as 1918. Gardner (14) found yellows to be the most serious disease of celery at Lafayette and Indianapolis, Ind., in 1919 and reported the disease as destructive in the Goshen district in 1914.

Rose (39) observed 50 per cent loss from yellows in a three-acre field of celery in Washington County, Minnesota, in 1921. Thomas (45) in 1921 reported an 8- to 10-acre planting ruined by root rot at Lodi, Ohio. Yellows has since become rather general in both the Lodi and Willard districts of Ohio, and the destructiveness of the disease in these sections is shown by Wilson's recent reports on its importance (56, 57, 58).

One grower in Niagara County, New York, lost 100,000 plants from yellows in 1922 (49), and in the same year Beach (49) observed a loss of from 5 to 25 per cent in plantings of Golden Self-Blanching in two Pennsylvania districts.

The increasing prevalence of yellows in Colorado was reported by Peitersen in 1923 (37), and LeClerg (22) noted a 40- to 50-per cent loss in some

fields at Canyon City in 1930. The increasing hazards of crop losses from this disease have made it necessary to discontinue the culture of susceptible varieties in portions of the Denver and Canyon City districts.

The recent spread of Fusarium yellows into the delta section of California has already been followed by serious losses to many growers. With Dr. J. B. Kendrick the senior author observed fields around Lodi, where the disease had dwarfed or killed from 10 to 70 per cent of the plants. Dr. Kendrick estimated that at least half of the acreage in the Lodi section showed the effects of yellows in 1936. The spread of the disease into this section and its increasing importance both there and in southern California is the most significant development in the recent history of Fusarium yellows.

SYMPTOMATOLOGY

Two distinct forms of celery yellows are described in this section, and a third is discussed briefly, for, although only recently discovered, it seems to differ from the others in enough characteristics to be classified as a separate form (30). The two forms described in detail are widely distributed and have been observed in all celery districts of Michigan where Fusarium yellows occurs extensively. In sections where the disease has been only recently introduced, only one form may be present. These two forms of Fusarium yellows are, for convenience, designated by the Roman numerals I and II. As will be discussed later, these disease aspects are associated with Fusarium pathogens which are distinguishable by appropriate cultural methods. For years the occurrence of two types of Fusarium yellows was not recognized, and it was not until a critical study had been made with plants grown under controlled conditions that the existence of distinct forms of the disease was determined. Once these observations were made it was easy to confirm the laboratory findings in the field.

In applying the descriptions given here of yellows-infected plants, and especially in examining plants in the field, it must be remembered that a diseased plant may show the effects of combined infection by both pathogens. In such instances, the signs are a combination of those that characterize the two forms of yellows. Gradations and overlappings of the characteristics that distinguish these forms may be observed in individual plants. At Kalamazoo, except in those fields where only one of the pathogens is present, it is more difficult, on the basis of plant reaction alone, to segregate infected plants into the two classes. Each pathogen has, in pure culture inoculations, consistently evoked characteristic signs. Diagnosis may be accurately made except in late stages when those characteristic signs tend to converge.

CHARACTERISTICS OF FUSARIUM YELLOWS FORM I

Seed Bed Effects

Seedlings grown in greenhouses for early plantings are sometimes attacked by yellows. In normal seasons this seldom occurs if proper temperatures for the production of good seedlings are maintained. However, in seasons of abundant sunshine, when air temperatures are more difficult to control, and in poorly managed houses Fusarium yellows may be an important disease of young plants.

The earliest effect of the disease observed in seedlings is a lag in the rate of growth. This may occur in limited areas of the seed bed, usually

in those portions of the bed subject to rapid drying. When air temperatures are below 70° C. the stunted condition of the young plants may be the only noticeable effect, and this may continue without much change unless the temperature rises. At higher temperatures, color changes in the leaflets of infected plants soon become evident. The green color of the foliage gradually blanches to a golden yellow, starting first as a faintly visible, mosaic-like mottling. (Pl. V: 3). The blanching is confined to the intervenal tissue of the leaflet (Pl. III: 2-B_1). Under favorable conditions the leaflets of small seedlings may curl downward slightly at the edges, but usually no such flexing is evident. Usually the plants succumb quickly at favorable temperatures. If the progress of the disease is slow, complete blanching of the green color in the leaflets may occur before the plant dies.

Another feature of the disease in seedlings is what appears to be typical damping off (Pl. V: 2). The young plants wilt and die suddenly, often without showing any foliage effects. An examination of the affected plants reveals no lesions at the soil level like those on plants infected with typical damping-off pathogens. Instead, the wilting and death of the seedling is preceded by an extensive decay of the root system. Infection occurs mostly through the tips of lateral rootlets, and a progressive decay continues until frequently only the tap root remains in a functioning condition.

In some seedlings only the tips of the fibrous roots are affected. A brown or reddish decay of the apices of those roots takes place and, depending upon the temperature, the effect upon the general appearance of the plant may be a dwarfing, a yellowing, or a combination of these. Some strains of the pathogen which cause form I of yellows excrete an extremely potent toxin, and if only the root tips are invaded, a blanching of the green color occurs when the air temperature is above 70° F. At lower temperatures stunting is the most common effect that is observed.

Field Aspects

The field symptoms which depict the various stages in the development of Fusarium yellows are discussed in full on the basis of many years of observation. In Michigan these are best seen in July and August when soil and air temperatures are most favorable for their expression. The normal seasonal development of the disease may be advanced or retarded by departures of temperature. In 1933, for example, all stages of the disease, from slight stunting to death of the plants, could be observed in June.

The general aspects of yellows in field plants are those which are characteristic of a progressive, systemic disease. After infection occurs, if soil and air temperatures are favorable, the disease develops in a typical way, and all those signs which depict the reactions of the infected plant are displayed in a more or less regular sequence. Changes in temperature and moisture are usually quickly reflected in the reactions of infected plants, with corresponding influence in the disease picture. The subdivisions which are utilized to segregate the various descriptive phases of Fusarium yellows take up the symptoms of the disease in an order that, to a certain degree, follows the usual disease course.

Stunting

In the earliest stages of the yellows disease the most noticeable characteristic of affected plants is a retarded growth rate. Except in hot weather this stunting effect can be observed before any definite foliage symptoms appear.

The dwarfed condition of infected plants is usually such an outstanding feature of the disease that Coons (3) called it "The stunting disease of celery." As applied to all varieties, green and yellow, dwarfing is probably the most constant and general symptom exhibited by infected plants. In green varieties, which seldom show any color changes in the leaflets, the stunted condition of the plants is the most common external evidence of infection. After infection occurs, the slower growth of the plant becomes more and more evident, and by the time the foliage symptoms appear in the self-blanching varieties, actual growth, as measured by an increase in the size of the plant, has practically ceased.

The stunting effect of the disease is most pronounced in young plants, and if infection occurs after the plants are half grown, dwarfing is not so apparent. Groups of stunted plants are usually the first observed effects of yellows in a field (Pl. I: 6; XVIII: 3). These groups of diseased plants form "spots" which usually are more or less circular in outline, and the seasonal spread of the disease can be charted by observing their radial enlargement from year to year (Pl. VIII).

Blanching

Following the initial dwarfing effects that result from infection, certain color changes occur in the leaflets. These changes are initiated and proceed in a manner that is typical of this form of yellows, and they represent the most useful and definite method of separating the two forms of disease in the field. The color changes at a rapid rate if air temperatures are high, and conversely, low air temperatures inhibit the blanching effects in the leaflets.

The first change that is noticeable after infection has occurred is a slight dullness in the glossy appearance of the leaflets. This effect is usually first apparent in some of the older leaves. This should be noted particularly, for the localization of the initial effects that are visible in the leaflets represents a distinct difference between form I and form II. As will be shown later, in form II the older leaves usually do not manifest the first color changes. If closely examined at this stage, it will be seen that the fading of green color in the leaflet is due to small flecks of chlorotic tissue which develop in the intervenal portions (Pl. V: 3). This chlorosis may be localized and begin at the edge of the leaflet or it may be more general. If temperatures are favorable, the green color progressively becomes paler, and the leaflet soon assumes a mottled appearance with a definite pattern of green and yellow. At this stage of blanching the green color is confined to the veins and the chlorotic islands of tissue are entirely intervenal in their placement (Pl. III: 2-B_1). A little later the green color disappears from the lamina, but the veins remain pale green for some time after the intervenal tissues are decolorized. Finally, the veins lose their green color also, and the entire leaflet approaches a uniform Straw Yellow[6] shade (Pl. III: 2-B_1). In the last stages decolorization proceeds further and the leaflet is Cream Color. Sometimes wilting occurs before this condition is reached.

At no time preceding or during the blanching stage is there normally any flexing of the leaflets; they remain in a normal, distended position (Pl. III: 1-A). This absence of curl is another distinguishing difference between

[6]Ridgway, Robert. Color standards and color nomenclature. 111 + 43 pp. Pls. 1-53. Washington, D. C. 1912.

form I and form II. The blanching effects of the disease spread to all leaves of an infected plant, but the symptoms may not appear in all the branches if unilateral infection occurs after the plant is more than half grown. With the most virulent strains of the pathogens and favorable temperatures, the progress of the disease is rapid, and only a few days may elapse from the time the first signs of decolorization appear until this effect has spread to all the leaves of the plant. In some infection tests with pure cultures and optimum temperature, the initial color changes have been observed as early as 10 days after the plants were placed in contact with the fungus.

Vascular Discoloration

The discoloration of the vascular elements of roots, crowns, and petioles is of constant occurrence in plants affected with Fusarium yellows (Pl. II: 5; Pl. IV: 5, 6). The browning or reddening of the vascular tissues extends from the ends of the invaded fibrous roots to the taproot, thence upward to the crown, and may, in some instances, reach the petiole (Pl. II: 5) and even the leaflets. The course of the invading pathogen may be followed by tracing the discolored elements from the infection court into the taproot and upward to the crown. Apparently, the discoloration of the vascular tissue is coextensive with the vertical penetration of the pathogen. Sometimes only the extreme upper portion of the taproot and the crown tissue are affected. In these instances the pathogen entered a lateral root close to the crown. Frequently the invaded secondary root decays, leaving only a stub to mark the place where the fungus entered.

Not infrequently evidence of unilateral invasion is seen in the localization of discolored tissue. When this is observed the primary invasion has taken place through one of the secondary roots which originates from some portion of the taproot close to the crown. The discoloration becomes more generalized if the fungus travels very far in the taproot before reaching the crown.

The crown tissue of the infected plant is sometimes the site of an extensive decay (Pl. IV: 5, 6). This lesion is a common feature of yellows in certain stages of the disease. It has been called "crown rot", and reference has been made to the reported association of bacteria with it (20). Certain plants die suddenly in the field or show symptoms of wilt, which usually is an immediate precursor of death. When cut open, many of these plants contain a crown cavity lined with shreds of dark brown, vascular tissue. In other instances the entire crown is honeycombed with strands of brown, spongy tissue. Sometimes a cleavage occurs which extends to the surface and exposes the reddened and fibrous condition of the crown. This phase of yellows has not been observed in infection tests with pure cultures, although a dry and spongy rot has frequently followed invasion of the crown by the fungus of form I. It seems probable that crown rot is initiated by the yellows pathogen and that other fungi, and possibly bacteria, are accessory agents in producing cavities.

Frangibility of Leaflets

At a fairly early stage in the development of the disease the leaves of infected plants become brittle. This characteristic is strikingly evident in some plants, and when such a plant is crushed between the fingers the sound is somewhat like that from dry leaves crushed in the hand. The growers say

the leaves are "glassy." This condition is not easily determined in seedlings nor in the early stages of the disease in older plants. The frangibleness of the leaves is most strongly developed in older leaves at about the time decolorization is starting. The green celeries develop the brittleness to a marked degree and, together with dwarfing, this furnishes the only apparent evidence that plants of these varieties are affected with the disease. Infected plants appear to be extremely turgid and erect (Pl. II: 3, 4) when they show this brittle condition. While brittleness of the leaflets is characteristic of both form of yellows, it is more strongly developed in plants infected with the fungus that causes form II.

Root Rot

Decay of the fibrous and fleshy roots of celery plants affected with yellows is a common symptom of the disease. Many Kalamazoo growers use the terms "root rot" or "root disease" in discussing the characteristics of the yellows disease. The extent to which the root system is affected varies greatly and is dependent upon soil temperature, soil moisture, the susceptibility of varieties, and the various strains of the causal fungus. In the most susceptible varieties, the fibrous roots of small plants may be entirely destroyed (Pl. IV: 1). Usually, however, there is a less extensive decay, and many of the roots on even badly diseased plants appear normal. When seedlings are transplanted into infested soil from the latter part of June to early August soil temperatures have usually reached an optimum for infection, and invasion may occur through the broken ends of the roots. Following this, there often occurs a progressive decay of these roots which may terminate in their complete destruction (Pl. IV: 2). The decayed portion of the root is dark brown to reddish brown and usually of a soft consistency.

Sometimes decay proceeds in such a manner that the cortex easily sloughs off from an infected fibrous root. Again the affected area may be restricted to the tips of the roots, and large numbers of the otherwise white, fibrous roots are affected with a typical, reddish-brown, apical decay. This can represent merely an early stage which later proceeds to a more extensive decay. Some phases of root decay may not be due solely to the yellows pathogen. Other species of Fusarium have been isolated from decaying root tissues, and often they have penetrated as far, or farther, into the root as the yellows pathogens.

Following the destruction of portions or of all the fibrous roots, the affected plant usually dies but sometimes there is a surprising recovery. Such occurs when rains and low temperatures succeed a period that has been especially favorable for the rapid development of the disease. Affected plants compensate more or less for the destroyed root area by producing adventitious roots above the affected area. If conditions are unfavorable for the development of the plant and conducive to the rapid progress of yellows, balance is not maintained and the plant dies. Low air temperatures apparently retard the toxic effects of the excretory products of the fungus, and as the new root system begins to function, the plant recovers its normal appearance and begins to grow at an accelerated rate. While the recovery is seldom permanent, because of relapses which occur when soil and air temperatures again rise, the plants frequently continue to function throughout the season and reach maturity much reduced in size. Such plants are, however, seldom of marketable quality.

Other Symptoms

At a certain stage in the development of the yellows disease, the leaves and petioles of affected celery plants develop a bitter taste. At times this is so pronounced that it is comparable with that of quinine. Celery normally becomes slightly bitter in very hot weather, and it is also during periods of high temperature that the bitterness of diseased plants is greatest. The bitter taste of affected plants, however, is far more intense than that which is characteristic of normal plants during even the hottest days. This quality of the tissues of diseased plants is most noticeable at about the time the rapid blanching stage is reached.

When the roots and crowns of diseased plants are cut open a characteristic odor is noticed, but it is difficult to define. To some it is fish-like, but this does not properly describe the pungent odor that is emitted. It is different from the odor of celery decayed by soft rot bacteria or by Septoria and is distinctive for plants affected with yellows.

Secondary Growths

Initiation of secondary growths is frequently observed in field plants affected with yellows. Adventitious buds are stimulated to develop when favorable growing weather follows a period when soil and air temperatures have hastened the development of yellows. Generally, extensive destruction of root tissue has occurred, but the plant has managed to survive until the change in weather conditions enables it to become re-established through the formation of secondary roots close to the crown. After these roots are formed, dormant buds are activated and the leaves which push out result in the formation of a multiaxillary plant (Pl. IV: 4).

The supernumerary petioles that are formed are frequently twisted and intertwined (Pl. IV: 3). They are similar in appearance to those described by Severin (41) in celery plants infected with the western strain of the virus of aster yellows. The petioles are sometimes split vertically near the base. As a result of the accessory growth two or more crowns may be present.

Wilting

While wilt has been mentioned in connection with certain other phases of yellows, particularly crown rot, it is the final stage of yellows. If the disease runs its full course, a complete collapse of the infected plant occurs (Pl. I: 7). In all instances where the plants are killed by the disease, the final phase is characterized either by gradual or sudden wilting. With the majority of infected plants, the chlorotic phase is succeeded by a period during which there is a gradual drying of the tissues. This is the common picture of yellows in hot, dry weather when the various phases succeed one another in a regular sequence. In general, subnormal temperatures retard the chlorotic phases and thus prolong or even subvert the wilting stages. Very high air temperatures accelerate the chlorotic changes and hasten the onset of the wilting stage. Although wilting is one of the characteristics of Fusarium yellows, it is always the end point of the infection, and because of the types of recovery described, it is by no means a general symptom. On this account, the name "Fusarium wilt of celery" is less appropriate than "Fusarium yellows."

CHARACTERISTICS OF FUSARIUM YELLOWS FORM II

Celery plants affected with the two forms of yellows show many similarities but there are also certain recognizable differences. Only those phases will be discussed in which distinctive signs are evident. Comparisons have been made of field-grown plants and those infected with pure cultures and grown under controlled environmental conditions. The differences have been constant and are always plainly evident in infection tests with pure cultures. It has already been pointed out, that, in the field, plants may become infected with both pathogens, and the symptoms displayed will not be those of one form of the yellows disease but a combination of the two. In these plants the symptoms are dependent upon many factors, such as, which pathogen first invaded the plant, relative rate of its growth in the plant, and the potency of the toxic substances excreted. The toxic effects are greatly modified by air temperatures. The fungus associated with form I produces a toxic substance which affects the plant much more rapidly at high temperatures than the excretory products of the other.

Curling of Leaflets

The effect upon the position of the leaflets and upon the manner in which the blanching develops constitute the two important features in which form II differs from form I. The earliest noticeable foliage effect in Fusarium yellows, form II, is a slight downward curling of the leaflets (Pl. III: 1-B). The youngest heart leaves are the first to show this flexing and they develop it strongly before a similar effect is seen in the older leaflets. At first the flexing is slight, but as the disease progresses it becomes more pronounced and in some of the leaflets the angular displacement of the apex may exceed 90 degrees. A distinct cupping becomes evident at the tips as the edges curl more and more. When the flexure reaches a maximum, the leaflet is distinctly convex on the ventral surface and deeply concave on the dorsal (Pl. III: 1-B).

In older leaflets, curling does not become so pronounced until after chlorosis has become apparent. The degree of curling, moreover, is less intense in many of these leaflets, but in some it equals that seen in the young heart leaves. It should be noted, that in this form of Fusarium yellows, the earliest symptom—curling—is manifested by the youngest leaves of the plant, while in form I it is the older leaves which show the initial effects as a blanching of color from the intervenal areas of the leaflets. If the soil is dry and the air and soil temperatures are high, field plants may develop a strong up-curling of the margins of the older leaflets (Pl. II: 3, 5). These leaflets are usually frangible. The young leaflets are always curled downward and are not brittle like the older ones. The up-curling of the older leaflets is entirely a field response, for it has not occurred in plants infected with the form II fungus under controlled conditions.

Blanching

Soon after the leaflets begin to curl, decolorization begins, but it is always first seen along the veins. The green color begins to disappear, usually first from the midrib, and becomes Straw Yellow progressively in the entire network (Pl. III: 2-B and C). Even the smallest branches in this network are decolorized to a clear yellow while the intervenal areas are still a normal green. The Straw Yellow pales now to Cream Color, which

is noticeable first in the midrib, and then extends gradually to all other parts of the leaflet. The areas immediately adjacent to the larger veins also begin to lose their green color, and narrow bands of tissue on either side of the blanched veins are decolorized. At this stage most of the intervenal tissue is still a normal green. The leaflet now presents an appearance which is in strong contrast to one at a similar stage of development on plants affected with form I. The parts of the leaflet decolorized are, in fact, just the opposite of those affected in form I, the blanching sequence being reversed.

From this stage onward there is a gradual extension of the blanched areas into the green portions between the veins. Different hues of yellow are always discernible in the blanching tissues. The veins which were first affected are much paler than those in which blanching began later, and all gradations are also observed in the intervenal tissues. In the final stage, the leaflet is blanched to Cream Color (Pl. III: 1-B). The end point is now similar to that shown by leaflets from plants affected with form I at a similar stage of development.

One noticeable difference between the two forms of yellows is the condition of the heart leaves in the late stages of the disease. In form II these leaves remain green until the final stage of yellows is reached (Pl. III: 1-B). Even when wilting has begun, the heart of the plant frequently is still green, although the veins of the leaflets may show the decolorization. Although the initial symptoms were evident as a flexing of the youngest leaflets, it is the heart leaves which retain longest the green color like that in healthy leaves. This may be due to a continuation of growth and the formation of new heart leaves. Even if no additional leaves are formed after infection occurs, and though the older leaves are decolorized, the green condition in the heart leaves persists. Thus, an examination of plants in the final stages of the disease may still disclose with which form of Fusarium yellows they are affected.

THE CALIFORNIA FORM OF YELLOWS

The form of yellows produced by the Fusarium isolated from stunted celery plants collected at Venice, Calif., in March 1934, appears to differ from the two forms of the disease in Michigan. Insufficient work has yet been done with this form to prove definitely that it is distinct. In the field no foliage symptoms were observed, and the only indication of infection was the small size of the plants in comparison with the healthy ones. The vascular system of the roots was discolored in a typical way, and aside from the lack of color changes in the leaflets the plants presented a normal picture of the yellows disease. At the time the plants were collected no significance was attached to the abnormal foliage symptoms, for the air temperatures were lower than those at which the color changes in the foliage proceed at a normal rate. About 10 days earlier, however, there had been a period of hot weather when the maximum temperatures were above 90° F.

Isolations were made from stunted plants collected in one field, and cultures of Fusarium were obtained which appeared to be similar to those isolated from plants affected with form I in Michigan. Infection experiments have been conducted with these cultures, and with strains which were reisolated from plants infected with the parent strains. The plants infected with these cultures have not shown the typical foliage symptoms of yellows. There is usually no decolorization of the leaflets, no curling, nor other symptoms that are characteristic of plants infected with the pathogens of

form I and form II. After infection occurs the plants do not grow so rapidly, but they retain their normal appearance. After a prolonged period of more or less sluggish growth the infected plants usually wilt and die. An examination discloses an extensive decay of the secondary roots, and sometimes the apical portion of the primary root is destroyed. The vascular system of the primary root is commonly invaded into the crown and similar in appearance to that of plants affected with the other forms of yellows.

HISTOLOGICAL EFFECTS OF THE DISEASE

In the sections made from plants affected with each of the two forms of Fusarium yellows, no important differences in the general histological features have been observed. It would seem that outstanding differences might be expected to occur in plants which show such contrasting symptoms. A more extensive comparison with material in all stages of the yellows disease, particularly the early ones, may reveal more than has been observed in these studies, which are based mostly on sections from roots of plants grown in the field. The roots were killed in forml-acetic-alcohol solution, imbedded in paraffin, sectioned and stained either with safranin and Delafield's haematoxylon, or phloxine and anilin blue.

Vascular Mycosis

Hyphae of the invading fungi are found in the vascular tissues of the roots in all celery plants that show typical symptoms of yellows, but under certain conditions the amount of invaded tissue may be comparatively small. Vascular mycosis is, however, the most important and constant microscopic feature of the disease. The hyphae are invariably found in some of the vessels. The general appearance of infected roots is similar to that which has been described in other plants infected with the vascular-invading Fusaria (Pl. VI: 1). The extent of vascular occupation by the hyphae, the presence of possible protective substances, like gums, and the occurrence of other organisms in the tracheae agree in general with the pathological features of fusarial wilt diseases. Especial attention has been given in the microscopic studies, however, to the presence of bacteria in the vascular tissue, since these organisms have frequently been reported as the causal agent or as an accessory pathogen in the yellows disease.

The number of hyphae in the tracheae of infected roots varies greatly. Some of the vessels contain only a single strand, while others are occupied by so much mycelium that the lumen is completely occluded (Pl. VI: 3). Relatively so few tracheae are plugged that there can be no serious interference with the transport of water. In no instance has sufficient stoppage of the water channels been observed, even in badly diseased roots, to account for the wilting which occurs in the late stages of the disease. Occasionally, in older roots the number of vessels occluded with hyphae and other materials are quite numerous, but in these plants wilting may not occur even though the plant continues to show typical symptoms of yellows until the end of the growing season. Again, young plants may pass through the wilting phase and die when the roots contain only a relatively small amount of mycelium. Thus, it seems that the evidence from a study of root sections is a further indication that mechanical stoppage of the conducting elements is not responsible for the wilt that develops in the late stages of the yellows disease. The hyphae within the tracheae are frequently swollen and vesic-

PLATE I

1. The initial appearance of Fusarium yellows in a field of short strain, Golden Self-Blanching celery. Season, 1920.

2. A portion of the same field in 1921. Soil infestation almost complete in the second year.

3. The first appearance of yellows in a field of Golden Self-Blanching celery as a result of planting infected seedlings.

4. A "spot" in a field of Golden Self-Blanching celery at Kalamazoo, season of 1916. The circumscribed area in which diseased plants occur represents the extent of soil infestation for the current season.

5. Thin stand and dwarfed plants of tall strain Golden Self-Blanching celery as result of Fusarium yellows. Kalamazoo, 1921.

6. Celery plants dead and dying of Fusarium yellows to form a "spot" in a field of Golden Self-Blanching, Mason, Mich., July 1921.

7. Yellows in a planting of Golden Self-Blanching (tall) at Comstock, Michigan, August 1933. A test planting of Michigan Golden in the foreground.

8. A five-acre planting of Golden Self-Blanching (tall) ruined by yellows at Comstock, Mich., August 1934.

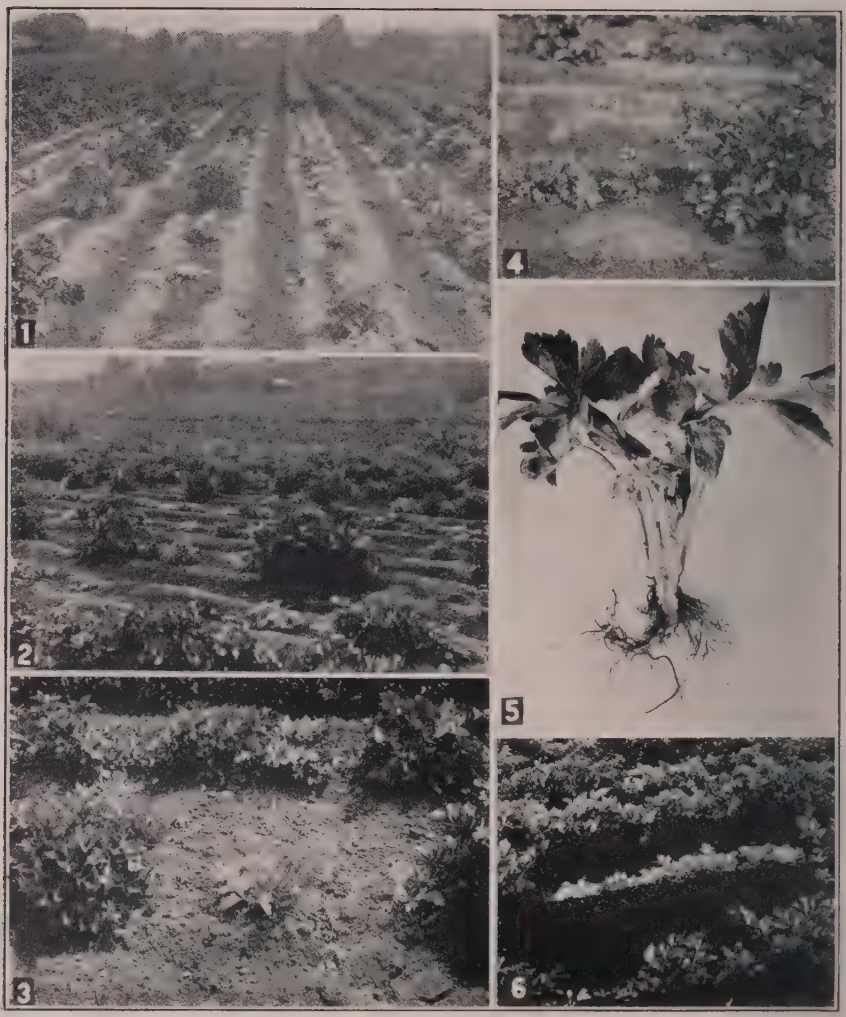

PLATE II

1-2. The stunting and chlorotic effects of yellows infection in Golden Self-Blanching celery. The large plants mostly are resistant green rogues. The soil is dry and the plants display the typical aspects of the disease in hot and dry weather. Kalamazoo, 1916.

3-4. Stunted and yellowed plants of Golden Self-Blanching celery which show the erectness of the petioles and up-curling of the leaflets in hot and dry seasons. The leaflets of these plants are very brittle.

5. Vascular discoloration in tap root, crown and petiole of a Golden Self-Blanching celery plant as a result of yellows infection. The decay of secondary roots is also apparent. Form II, yellows.

6. Golden Self-Blanching plants which became infected in the seed bed and which display the stunting effects of yellows. Late stage of chlorosis just preceding the wilting phase.

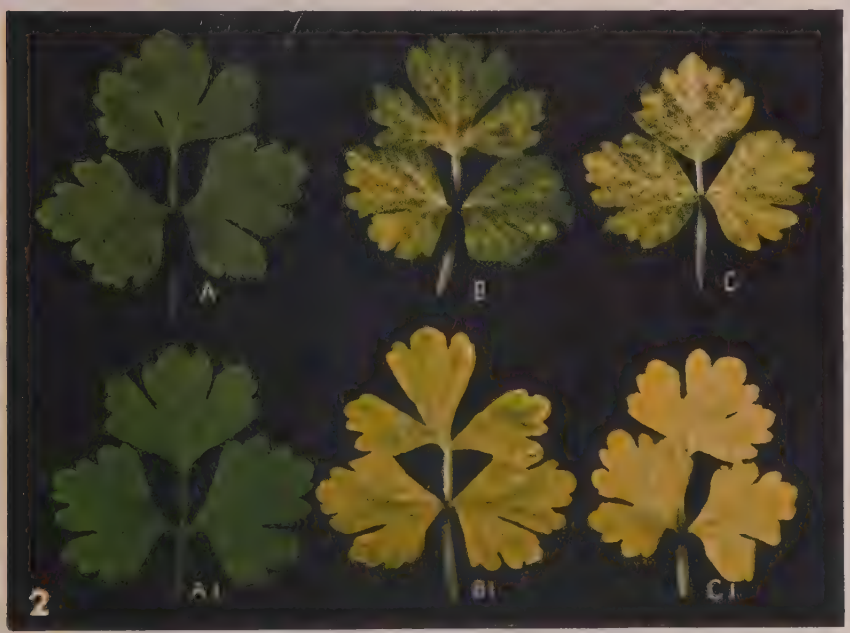

PLATE III

1. Form I (A) and form II (B) of Fusarium yellows in Golden Phenomenal celery. There is no flexing of the leaflets in form I and the chlorosis is intervenal. The leaflets are curled downward and the veins show the first effects of chlorosis in form II.

2. The comparative chlorotic effects of two forms of yellows in the leaflets of Golden Phenomenal celery. In form II (B, C) the veinal discoloration is most prominent, while in form I (B_1, C_1) the veins remain green until the final stage of chlorosis is reached. Normal leaflets (A, A_1) for comparison.

PLATE IV

1. Normal and diseased plants of Golden Self-Blanching showing extensive destruction of roots by the yellows disease.
2. Decaying secondary roots which originated near the crown after the primary root was destroyed by yellows.
3. Twisting and intertwining of petioles in a Golden Self-Blanching celery plant affected with yellows, form II.
4. A multiaxillary celery plant developed from adventitious buds activated as a result of root destruction by Fusarium yellows.
5-6. Crown rot in Golden Phenomenal celery. This phase of yellows is usually most pronounced in plants infected by the form I pathogen.

PLATE V

1. Yellows starting in seedlings of tall strain Golden Self Blanching celery. The type of chlorosis and the absence of curl in the leaflets indicates that the plants are infected with *Fusarium apii*.

2. Apparent "damping-off" of celery seedlings caused by root destruction which sometimes occurs when the plants are grown in heavily infested soil.

3. Mosaic-like mottling in Golden Self-Blanching celery seedling as a result of infection by *Fusarium apii* var. *pallidum*.

4. A yellows-resistant celery plant in flower.

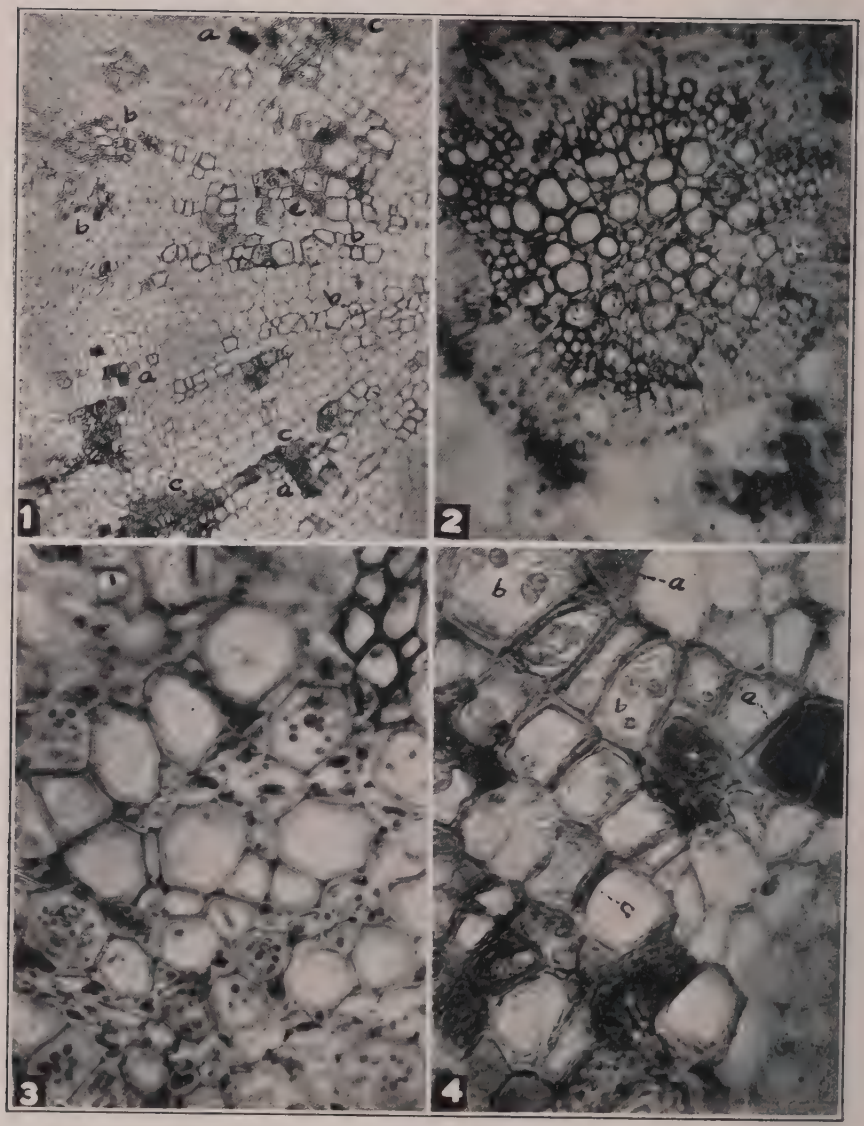

PLATE VI

1. Transverse section of primary root of celery plant affected with Fusarium yellows. Tracheal gummosis (a); discolored tracheal walls (b); vascular mycosis (c). Unstained section, 120X.

2. Transverse section of primary root of celery seedling affected with yellows. The tracheal mycosis is somewhat localized but vessels bordering the cambium region are invaded by the pathogen. Delafield's haematoxylon stain, 200X.

3. Transverse section of primary root in celery seedling affected with yellows showing extensive invasion of the tracheae in the metaxylem. Delafield's haematoxylon stain, 800X.

4. Transverse section of primary root of field-grown plant showing tracheal gummosis (a); tracheal mycosis (b); and tracheal bacteriosis (c). Unstained section, 800X.

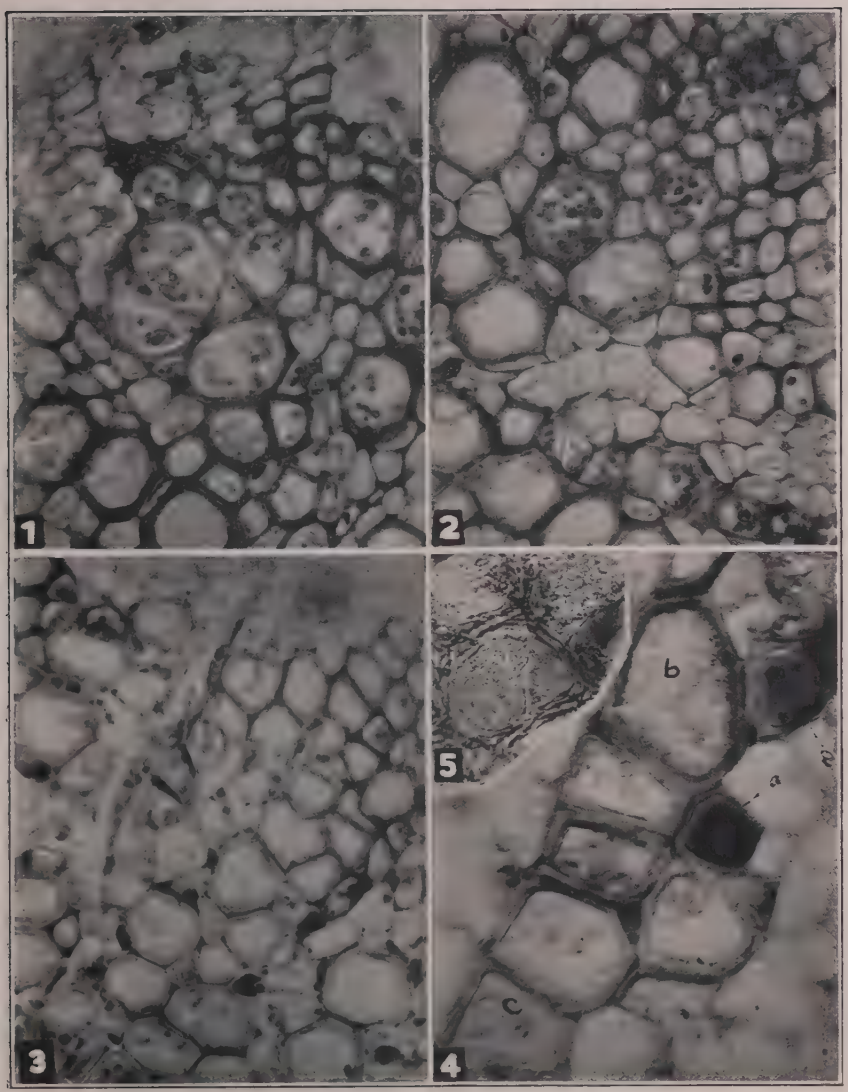

PLATE VII

1. Section of primary root of seedling in which the tracheae in the transition region are extensively invaded by hyphae of the yellows pathogen. Delafield's haematoxylon stain, 800X.

2. Section of primary root of seedling affected with yellows. The tracheae bordering the pith rays and those near the phloem are invaded by hyphae.

3. Hyphae growing longitudinally through the pith ray of primary root. The direction of migration is uncertain but the hyphae can be seen in the phloem region. Delafield's haematoxylon stain, 800X.

4. Section of primary root of celery plant with tracheal gummosis (a); tracheal bacteriosis (b); hyphae imbedded in gum which fills the lumen of vessel (c). Unstained section, 800X.

5. Tracheae completely occluded by granular masses of bacteria in the root of field-grown plant affected with yellows. Unstained, 1000X.

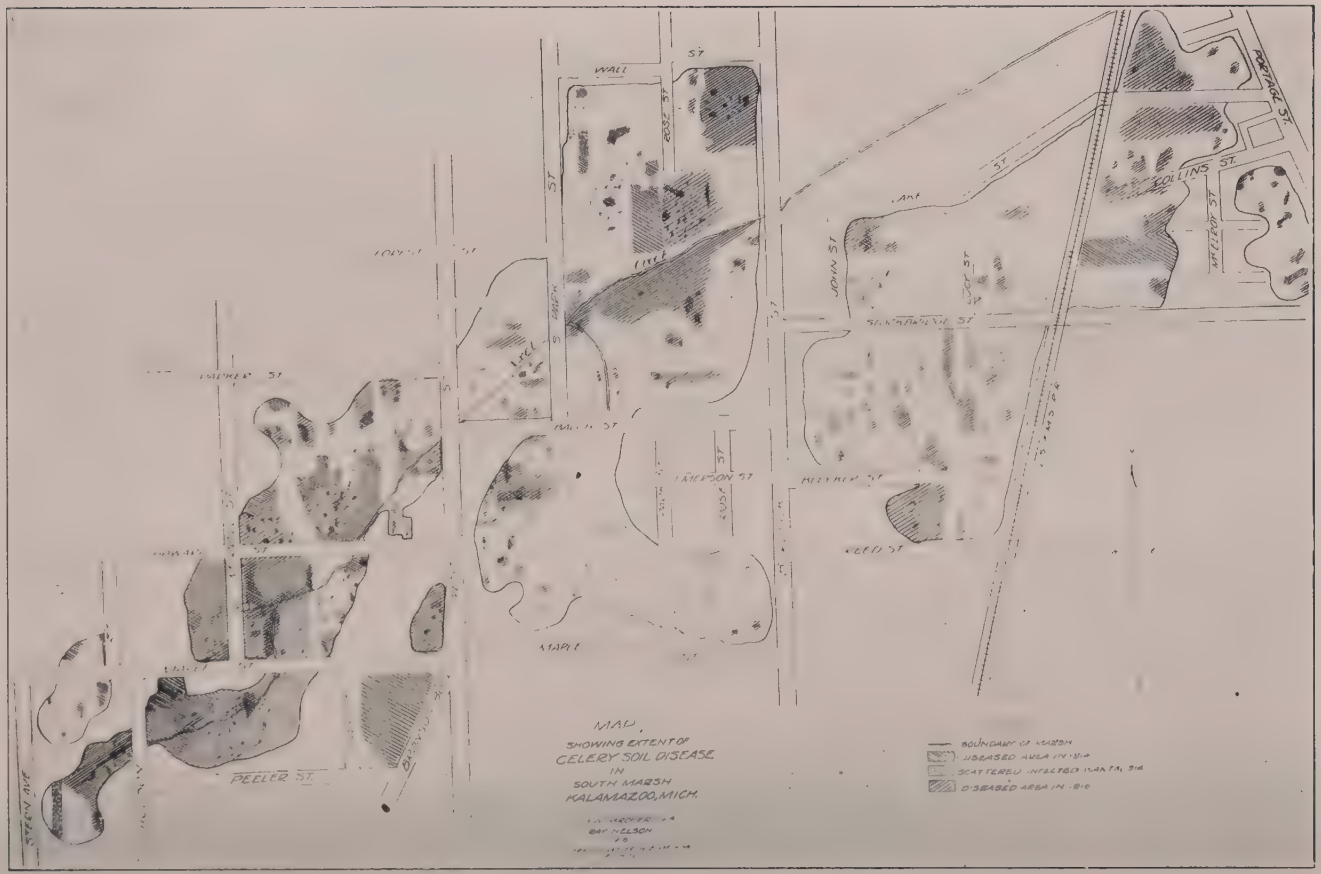

PLATE VIII

Map showing the extent of Fusarium yellows in the south marsh area at Kalamazoo in 1914 and 1916. The marsh is drained by Axel creek, and the overflow of this stream in June, 1916, submerged fields along its banks and greatly extended the infested area.

ular, and strands of short, swollen cells lie in a more or less coiled position, with their longer axes perpendicular to the walls of the tracheae. In general, the mycelium is coarse and follows a tortuous path through the lumina. In contrast with the fungus in artificial culture, the appearance of the mycelium in old roots is comparable to that of very old and vacuolated hyphae. In younger roots, and especially where the fungus is growing rapidly, the threads are finer and more uniform.

The mycelium frequently passes through the pits in the walls of the tracheae and invades the adjacent elements. Hyphae have been observed which pass into or between the cells of the xylem parenchyma and even reach the phloem (Pl. VII: 3). In infected young roots the hyphae may be very numerous in the tracheae that lie adjacent to the region of differentiation (Pl. VII: 1). In these roots the tracheae that border the pith rays also are strongly invaded (Pl. VII: 2). It appears probable that the fungus absorbs food materials from the phloem and that the xylem is mostly an avenue for the rapid vertical invasion of the plant. The unobstructed lumina of the tracheae provide an ideal pathway for migration of the fungus within the plant. It is doubtful if the solutes in the xylem alone could support the extensive and rapid multiplication of the mycelium in the root and other portions of the plant. The facility with which the hyphae leave the tracheae and the ramification of the mycelium in the xylem parenchyma, together with the observed invasion of numerous tracheae close to the phloem, suggests the necessity of contact with extra-tracheal elements for the growth of the parasite. No condidia were observed in the vessels or elsewhere in the invaded tissues.

Tracheal Bacteriosis

In sections from roots of plants infected in the field, it is not uncommon to find from a few to many, tracheae filled with masses of bacteria (Pl. VI: 4; Pl. VII: 4, 5). Sometimes several adjacent vessels in a vascular bundle are occupied by short rods or coccoid forms of bacteria. The granular masses, which have been identified as bacteria through the staining reactions, are found in both the small and large tracheae, and occasionally in the xylem parenchyma. Bacterial pockets, or lysigenous cavities, are sometimes formed by a breaking down of the walls of the xylem elements. A single trachea filled with the organisms may be surrounded by others that are empty. Occasionally, in older roots the vessels which contain the bacteria are very numerous, but in younger roots the number of elements filled with the bacterial organisms are few in comparison with those occupied by hyphae.

In the roots of plants grown in soil sterilized before being infested with the yellows pathogens, the occlusion of vessels by bacteria has seldom been observed. Bacterial invasion of infected plants is, however, a feature of the disease in the field which requires further study. The number of vessels occupied by bacteria is small in comparison with the total tracheal complement of the root. Although it seems doubtful that the invasion of those relatively few elements could contribute much to the general reactions of the infected plant, there is a possibility that the progress or intensity of the disease is influenced by this phenomenon. It is certain that the bacteria are not the primary cause of the disease and that they cannot infect a normal plant. The Fusaria determined as the pathogens induce all the symptoms of yellows irrespective of whether the bacterial complication occurs. However, the ease with which a bacterial organism can be isolated from infected

celery plants and the difficulty sometimes experienced in obtaining cultures of the real pathogen is sufficient to show the close association of bacteria with plants that become diseased in the field.

Tracheal Gummosis

The occlusion of vessels with an amorphous gum-like material is a characteristic feature of sections from celery plants affected with Fusarium yellows (Pl. VI: 4; Pl. VII: 4). This condition is most common in plants grown in the field, and the number of vessels showing this type of occlusion appears to be directly related to the duration of the diseased condition and to the extent of the vascular mycosis. In most of the vessels that have been observed the gum occurs alone, but occasionally hyphae are also present (Pl. VII: 4). The gum is dark-colored and stains readily with some dyes. The significance or cause of gummosis is not understood, and the question has been raised as to whether the occurrence of similar, gum-like materials in the vessels of cabbage plants infected with *Fusarium conglutinans* is a response to the presence of the fungus or to injuries from other causes. Since the number of gum-occluded vessels is relatively large in some celery plants, and a similar condition has not been observed in plants free of the fungus, it seems probable that there is some relation between the gummosis and the presence of the fungus. Gum formation usually occurs as a result of injury. Its formation in the tracheae of celery plants infected with the yellows pathogens may have a protective effect. Vessels containing hyphae are sometimes completely circumscribed by gum-filled tracheae which effectively wall off the fungus from lateral invasion of the contiguous cells.

Changes in the tracheal walls are noticeable in the older roots, especially the taproot, which result in a browning and a refractory reaction to stains (Pl. VI: 1). Whereas the normal tracheae stain readily with those dyes that have an affinity for lignified tissue, some of the vessels in the taproots of affected plants do not take up the stain at all or hold it so weakly that the color is lost in dehydrating the material prior to mounting in balsam. Groups of tracheae in the proto-xylem appear conspicuously brown when examined under low magnification. At higher magnifications the individual vessels are seen to be filled with either amorphous or granular deposits colored like the walls. Hyphae are present in some vessels, free, or imbedded in the tracheal gum. The walls of some of these tracheae appear to be gelatinized or impregnated with material similar to that in the lumina.

ETIOLOGY

HISTORY

In his original report on celery crown rot, Stone (43) indicated that he believed the disease was bacterial in nature. In the more detailed account published the following year, he stated that observations indicated the disease was caused by bacteria which could be isolated without difficulty from diseased plants (44). No experimental proof of the causal relation of bacteria to the disease was submitted to substantiate the observational evidence. Coons (3) observed that the tracheae in the roots of diseased celery plants which he collected at Kalamazoo were occluded by bacteria. As a result of these observations, and of some preliminary infection tests, he considered the stunting disease (yellows) as bacterial in origin. A bacterium and a

Fusarium were isolated by Krout (20) from celery plants affected with crown rot in New Jersey. He believed that the disease was caused by the bacterium or by the component section of the two organisms. Rod-shaped and fusiform bacteria were reported by Butler (2) associated with internal, brown lesions of celery plants affected with yellows in Colorado. No detailed report on the investigational phases of this problem has yet appeared.

The senior author began work on celery yellows during the summer of 1916. Celery plants showing typical symptoms were obtained at Kalamazoo in July, and—using standard methods—attempts were made to obtain cultures of the bacterial organism suspected of being the cause of the disease. From some of these plants only Fusarium was isolated, but from others bacteria also appeared in the dilution plates. Later in the same season, isolations from additional plants yielded similar cultures of Fusarium. During the winter of 1916-'17 definite proof of the causal relationship of this Fusarium to the yellows disease was obtained in infection experiments. A brief preliminary report (11) on the etiology of the disease was given in 1921 after repeated infection tests had established the pathogenicity of the fungus associated with diseased plants.

Other workers have since associated a Fusarium with the disease. Gardner (15) did some work with a Fusarium isolated from celery in Indiana. Milbrath (24) isolated a species of Fusarium from plants showing symptoms of yellows at Chula Vista, Calif., but he made no report on its pathogenicity. Wilson (58) has proved the pathogenicity of Fusaria isolated from celery plants in Ohio, and Ryker (40) recently announced similar results with cultures obtained from diseased plants in Wisconsin.

PATHOGENICITY OF ISOLATES

Cultures of the Fusarium isolated from infected roots of Golden Self-Blanching celery plants in 1916 were used for the first infection tests. After pure cultures of the fungus had been obtained from single spores, the mycelium from these cultures was introduced into wounds made in the roots and crowns of young plants of the Golden Self-Blanching variety. The inoculated plants were placed in cold frames and observed for several weeks, but no symptoms of the yellows disease appeared. Subsequent tests demonstrated that this method of inoculation was unsatisfactory and that infection seldom occurred. The important influence of temperature was established in tests made a short time later and, in part, explained the failure of the first infection experiments.

Gilman's findings (16) on the relation of temperature to the occurrence of cabbage yellows seemed to furnish a possible explanation for the failure of the initial infection tests. In December 1916, these tests were resumed and the experience of Gilman was utilized as a guide in shaping the environmental conditions to which the plants were exposed. Instead of inserting mycelial inoculum into wounds in the crowns and roots, the roots of young plants which had been grown in sterilized soil were dipped in spore suspensions of the fungus and the plants then set in sterilized soil. Since no equipment for the control of soil temperatures was available, the flats were placed in a Wardian case in which the air temperature was held at approximately 28° C. Within four weeks these plants developed typical symptoms of yellows, and pure cultures of the Fusarium were recovered from discolored vascular tissues of roots and crowns. These preliminary experiments yielded suggestive evidence of the etiological relation of Fusarium

to celery yellows and demonstrated the importance of temperature to infection and development of symptoms.

Methods of Test

The experiments on the etiology of yellows were not resumed until 1919 when the disease was destructive in fields of celery near Lansing, and additional cultures of Fusarium were isolated from plants collected in this area. The results of the earlier tests were completely confirmed with the new isolates. In subsequent infection experiments at various times for more than 15 years, the causal relation of Fusarium to celery yellows has been proved with cultures obtained from plants grown in various sections of Michigan and in several other states.

Cultures of Fusarium are readily obtained from celery plants affected with yellows. Pure cultures can usually be isolated from vascular tissue by the usual technic if the disease has not yet progressed to the stage where other organisms may have invaded the parasitized tissues.[7] The usual procedure followed has been to isolate pure clonal lines from the mycelium growing on the plates. Hyphal tips of the fungus are excised with small, flattened, and sharp needles under a binocular, dissecting microscope at a magnification of about 25 diameters and each tip seeded on potato agar containing ½ per cent dextrose and 2 per cent agar. Inoculum for adding to sterilized soil was prepared by subculturing the pure lines of Fusarium on sterilized whole oats in wide-mouth, Erlenmeyer flasks. All soil used in growing the seedlings for the infection tests and for infestation with pure cultures of Fusaria was steamed for at least two hours.

In most of the tests conducted since 1928, temperature tanks with automatic controls have been utilized for maintaining a constant soil temperature. The soil cans used in these tanks were sterilized by soaking in a 1-100 solution of formaldehyde and then allowing them to dry. To each can containing sterilized, composted soil or muck, one-half of the inoculum contained in a one-liter Erlenmeyer flask was added and mixed thoroughly with this soil. Into this infested soil were set young and rapidly growing celery plants with roots that had penetrated to the walls of the pots in which they were grown. Four or five plants of susceptible varieties, usually Tall Golden or Golden Phenomenal, were set in each can. An inch or so of granulated cork was placed on the surface of the soil to conserve moisture and the plants were held in a cool place for two or three days to encourage the formation of new roots, after which the cans were placed in the tanks. The temperature of the water in which the cans were immersed was maintained at approximately 29 to 30° C. At this temperature the soil within the cans is kept at about 28 to 29° C. As needed, sterilized, distilled water was added to maintain a fairly constant supply of moisture.

Sources of Isolates

All of the cultures of Fusarium used in the experimental work previous to 1919 were lost during the war period. Additional cultures were obtained

[7] In making the isolations infected plants are first washed thoroughly and then placed in 95-per cent alcohol for a few seconds. The alcohol is burned off intermittently to prevent overheating of the interior of the plant. Bits of discolored vascular tissue are removed and seeded on prune agar. The prune agar inhibits the growth of bacteria and the mycelium of the pathogens is usually well-developed in three to five days at 25° C.

TABLE 1. *Index of Fusaria isolated from celery plants affected with yellows and used in the infection experiments and taxonomical studies.*

Isolate No.	Date of Isolation	Source
1	June 18, 1919	From primary root of Golden Self-Blanching plant (dwarf) obtained at Mason, Michigan.
2	Sept. 26, 1930	From primary root of "Tall Golden" plant collected at Kalamazoo.
3	Sept. 26, 1930	Same source as isolate 2, but cultured from a separate plant.
7	Aug. 23, 1929	Primary root of "Tall Golden" plant from Kalamazoo.
10	July 22, 1927	Primary root of "Wonderful" plant collected at Kalamazoo.
11	Mar. 6, 1929	Re-isolated from plant infected with isolate No. 3.
13	Sept. 29, 1928	From primary root of Golden Self-Blanching plant received from Littleton, Colorado.
17	Aug. 16, 1927	From primary root of plant collected at Lodi, Ohio.
21	Mar. 6, 1929	From root of plant infected with isolate No. 1.
24	Aug. 13, 1929	From crown of "Tall Golden" plant collected at Kalamazoo.
26	Apr. —, 1931	Crown of seedling grown in infested soil from Kalamazoo which had been air dried for 19 months.
27	Apr. —, 1931	Another plant from the same soil.
30	Apr. —, 1931	Another plant from the same soil.
32	Sept. 9, 1931	Isolated by A. G. Newhall from plant collected in Wayne County, New York, and received from him Oct. 11, 1931.
40	Aug. 20, 1931	Isolated from a Giant Pascal plant received from Canyon City, Colorado.
42	Sept. 30, 1931	Isolated by A. G. Newhall from Golden Self-Blanching plant collected at Rochester, N. Y.
45	Sept. 24, 1932	From Golden Prize plant (crown) collected at Kalamazoo.
46	Sept. 24, 1932	From petiole of Golden Prize plant collected at Kalamazoo.
49	Jan. 5, 1933	From crown of "Tall Golden" plant collected at Owosso, Mich., in July and which showed atypical symptoms in the field.
50	Jan. 5, 1933	From root of the same plant.
53	Mar. 21, 1934	From root of "Tall Golden" plant collected at Venice California.
54	Mar. 21, 1934	Plant No. 2 collected from same locality.
55	Mar. 21, 1934	Plant No. 3 collected from same locality.
64	1934	Isolated by J. D. Wilson from Golden Self-Blanching plant grown in Ohio.
68	Aug. 15, 1934	Isolated by C. D. Sherbakoff from Golden Prize plant collected at Comstock, Mich. This plant showed form I symptoms in the field.
69	Aug. 15, 1934	Isolated by C. D. Sherbakoff from Golden Prize plant showing symptoms of form II.
70	Aug. 15, 1934	From root of "Tall Golden" plant showing symptoms of form I and affected with crown rot.
80	Mar. 1, 1935	Re-isolated from Golden Phenomenal plant infected with isolate No. 72 (Isolate 72 cultured from plant received from Hamilton, Mich., Aug. 11, 1934. Not used in the infection tests reported in this paper.)
81	Mar. 1, 1935	Re-isolated from Golden Phenomenal plant infected with isolate No. 73 (Isolate 73 from plant No. 2 received from Hamilton, Mich. This isolate not used in experiments reported in this paper.)
87	Dec. 15, 1934	Re-isolated from root of Golden Phenomenal plant infected with isolate No. 7.

in 1919, and since that time more than 100 pure-line isolates have been cultured from diseased celery plants obtained from various parts of Michigan and from plants grown in other states. Cultures have been received from A. G. Newhall which he isolated from plants showing symptoms of Fusarium yellows in New York, and from J. D. Wilson which he isolated from diseased celery plants in Ohio. All these isolates have been subcultured as pure, clonal lines and the pathogenicity of each has been tested against plants of either Tall Golden or Golden Plume varieties. The isolates which proved to be pathogenic are those that have been used in the subsequent infection tests and in the taxonomic studies. Some of those strains have been lost, and the present collection consists of about 50 isolates of proved pathogenicity. Each isolate consistently produces a single form of the yellows disease, and, of those which have been cultured since the two forms were first identified, there are about an equal number which cause form I and form II, respectively. Included in the collection are the pathogens isolated from celery plants obtained at Venice, Calif., in March 1934, and also re-isolates of these original strains. The strains that appear

in the list comprise only those referred to in the infection tests and in the taxonomic studies. The accession number of each strain is that which was assigned to the original culture when its pathogenicity was first demonstrated. A number of other species and varieties of Fusarium used for comparisons in the pathogenicity tests and in the taxonomic studies, are listed in Table 2.

TABLE 2. *Index of other species of Fusarium used in infection tests and taxonomic studies for comparison with the celery Fusaria.*

Accession No.	Species	Source
496	*Fusarium conglutinans*	From J. C. Walker and isolated by him in 1924 from yellowed cabbage obtained at Racine, Wisconsin.
497	*F. conglutinans* var. *callistephi*	From H. W. Wollenweber (No. 1492) and isolated in Germany from wilted plant of *Callistephus chinensis*.
498	*Fusarium orthoceras*	From H. W. Wollenweber (No. 4971). Isolated in 1933 from diseased plant of *Callistephus chinensis* from Sweden.
499	*F. orthoceras*	From H. W. Wollenweber (No. 2443) and isolated by him from *Urtica dioica* in Saxony, 1925.
500	*F. conglutinans* var. *betae*	From Dewey Stewart (No. 102). Isolated from wilted plant of *Beta vulgaris* and used in the investigations reported in Phytopathology.
501	*Fusarium lini*	From Prof. Flor, Fargo, North Dakota, (No. 201).
502	*Fusarium lini*	From Prof. Flor, Fargo, North Dakota, (No. 203).
503	*F. orthoceras*	Obtained from Dr. J. Westerdijk, Wageningin, Holland. Isolated by H. W. Wollenweber in 1912 at Washington, D. C., from a root of diseased celery plant sent to him from Ohio.
504	*F. orthoceras* var. *pisi*	From J. C. Walker, Madison, Wisconsin. Received Mar. 17, 1935. Labeled No. 1.
505	*F. orthoceras* var. *pisi*	From same source. Labeled No. 2.

Etiology of Fusarium Yellows Form I and II

Infection experiments have been conducted during the last 14 years with pure lines of all the isolates obtained from diseased celery plants. A detailed account of one inoculation test with temperatures controlled will suffice to illustrate the methods employed in the infection experiments and the general character of the results obtained. The experiment outlined here was chosen because comparative virulent strains of the pathogens which cause the two forms of yellows were used, including both old and new accessions. It was also chosen because the cultures which were re-isolated from the infected plants were used in a later experiment to demonstrate the specific integrity of the various isolates in their relation to the two forms of the yellows disease.

In this test seven strains of the pathogens were used. Previous preliminary experiments had shown that four of these isolates produced form I, and three produced form II of yellows. The stock cultures, which had been maintained on potato hard agar, were subcultured on this medium in petri dishes. From the peripheral portions of the colonies hyphal-tip transfers were made to agar slants to eliminate all possibilities of mixtures. As soon as the fungi had developed sufficiently, transfers were made to sterilized whole oats, and when the mycelium had covered the grains in the flasks the cultures were used for infesting sterilized soil.

The soil used in this experiment was a rich compost which was screened and then steamed for two hours just previous to use. The necessary amount of this soil was added to 16 of the soil cans and into the soil in each of 14 cans was emptied the contents of a flask which contained one strain of the

pathogen growing on oats. The inoculum was stirred thoroughly into the soil with wooden pot labels. The soil in two of the cans was not infested and celery plants were first transplanted into this soil to which nothing was added but distilled water. Rapidly growing plants of "Tall Golden" were used which had been grown in sterilized soil. On Feb. 2, 1933, five plants were transplanted into each can from three-inch pots. After the five plants had been set in a can, the hands were washed thoroughly in a 1-1000 solution of corrosive sublimate before other plants were set in soil infested with another strain. The plants in each can were watered with approximately the same amount of distilled water, and the cans were placed immediately in the tanks adjusted to maintain a constant temperature of 29° C. The air temperature fluctuated at times, but an attempt was made to keep it as near 15° C. as possible. The maintenance of this temperature was essential to the success of other experiments being conducted in the greenhouses, and no attempt was made to hasten the development of symptoms by raising the temperature. The experiment was terminated on March 24, 50 days after the cans were placed in the tanks. The data recorded include the date when the first symptoms were noted and the number of diseased, dead, and healthy plants at the conclusion of the experiment. The internal condition of each plant was also determined by an examination of the roots and crown. The results are given in Table 3.

Of the 35 plants grown in the seven cans of infested soil, none escaped infection, and each plant displayed symptoms which were characteristic of only one form of the yellows disease. The foliage symptoms of the five plants

TABLE 3. *Pathogenicity tests of 7 strains of Fusarium isolated from celery plants affected with yellows. Soil temperature 28-29° C. Experiment began February 2, terminated March 24, 1933.*

Isolate No.	Appearance of First Symptoms	Condition of Plants Mar. 24, 1933			Symptoms Exhibited
		Diseased	Dead	Healthy	
1.....	Mar. 1, 1933	4	1	0	Surviving plants dwarfed. Foliage yellow, with sequential development of chlorosis typical of form I. Invasion through lateral roots. Stele in roots strongly discolored. Crown normal.
7.....	Feb. 24, 1933	3	2	0	Foliage symptoms typical of form I. Plants dwarfed. No wilting. Extensive decay in fibrous roots, stele discolored into crown.
10.....	Mar. 1, 1933	4	1	0	Only slight dwarfing. Foliage symptoms typical of form I. Especially intense discoloration in stele of tap root.
11.....	Feb. 25, 1933	3	2	0	Foliage symptoms characteristic of form I. Very intense vascular discoloration in two of the surviving plants. Some decay of secondary roots.
27.....	Feb. 28, 1933	3	2	0	Plants dwarfed and showing foliage symptoms typical for form II. Leaves much curled. Stele in tap roots discolored into crown of plants.
32.....	Feb. 28, 1933	4	1	0	Symptoms typical of form II. Leaflets curled downward; those in the heart still green. Typical discoloration in the stele.
50.....	Feb. 27, 1933	4	1	0	Foliage symptoms typical of form II with strong blanching effects first seen in veins. Plants much dwarfed and the leaflets curled downward. Stele reddened and decayed.
Controls.....		0	0	10	

in each can were similar. In no instance was there any difficulty in determining by the appearance of the leaflets which form of the disease was represented. There was some variation in the latent period of infection; the earliest symptoms were shown in the plants infected with strain 7. The minimum period of latency at this temperature was 23 days and the maximum was 26, a result which indicated that the pathogenic properties of these seven strains were alike. Ten of the infected plants died before the final records were made, and these developed the usual symptoms of wilting in the final phase of the disease. The control plants remained healthy.

Three diseased plants were taken from each of the seven cans and used for the attempt to recover the pathogens from the invaded stele of the roots. The plants were handled in the usual way and tissue plantings from the discolored vascular tissue were made to prune agar in petri dishes. After 48 hours mycelial growth was evident around each piece of the transplanted tissue and hyphal tips were excised and cultured on potato sugar. Pure line cultures on oats were used for infesting sterilized soil for a test of the pathogenicity of the re-isolates.

Of the cultures from the diseased plants, 26 were selected for pathogenicity and specificity tests. These 26 isolates represented descendants of six of the original seven strains. The re-isolates from plants infected with strain 10 were not used because of lack of facilities for handling so many cans in the tanks, and because isolates 10 and 11 were so similar in all respects that it seemed a needless duplication to test both of them. The infection tests of these re-isolates were conducted at different times. The cultures from plants infected with isolates 1 and 7 were tested from May 16 to June 6, 1933. Of the 14 strains in this infection test, 13 produced disease typical of form I; one strain appeared to be non-pathogenic. Each of the 13 pathogenic re-isolates was extremely virulent and symptoms appeared in the leaflets as early as 10 days after the plants were set in the cans. The air temperatures were relatively high, 25° C. or above, each day during the test, and the blanching of the foliage proceeded with rapidity. All plants in five of the nine cans in which the re-isolates of strain 7 were tested were dead on June 7, just 21 days from the beginning of the experiment. This extremely rapid, lethal effect of the disease had not previously been observed in infection tests and never occurs during the cooler months of the year when air temperatures are lower. All surviving plants, with the exception of those in one can in which the fungus appeared to be non-pathogenic, showed very typical foliage symptoms of yellows. Some of them displayed advanced symptoms, while others were less severely affected.

An examination of the surface and the interior of the roots of the yellowed plants disclosed a significant condition. In no instance was the vascular invasion commensurate with the severity of the foliage effects. Plants with conspicuous yellowing of the leaflets showed no internal discoloration of the tap roots, and only a slight invasion of the secondary roots. This condition was especially pronounced in the plants from cans infested with re-isolates of strain 7. The early appearing and striking effects in the foliage had been produced as a result of an invasion of the secondary roots, which, under ordinary conditions, would have hardly produced any noticeable changes in the leaflets. It was apparent from this condition that the virulence of the re-isolates was greater than that of the parent strains. It was also apparent, as had been known previously, that some strains of the fungus which cause form I of yellows, produce a toxin which is most effective at air

temperatures similar to those to which the plants were exposed in this test. The inactivation of the small amounts of root tissue which had been invaded by the fungus was certainly not the cause of the rapid and destructive effects of the disease. The strong virulence of the pathogens in this test could best be explained by assuming that the high air temperature had made their toxic products more effective.

The difficulty of controlling the temperatures of the tanks because of the high air temperatures in the greenhouse in June made it impossible to test the other re-isolated strains until December. The re-isolates of strains 11, 27, 32, and 50 were tested from Dec. 3, 1933, to Feb. 3, 1934. The conditions were the same as in the preceding experiment except that the air temperatures were much lower and, as a consequence, the foliage symptoms developed more slowly and the general progress of the disease was not so rapid. A summarized report of the final results of this test is combined in Table 4, with those of the experiment in which the re-isolates of strains 1 and 7 were used.

TABLE 4. *Pathogenicity and integrity tests of Fusaria re-isolated from plants infected with the parent strains in the experiment of Feb. 2-Mar. 24, 1933. Summarized results of experiments of May 16-June 7, 1933, and of Dec. 3, 1933-Feb. 3, 1934.**

Parent Strain	Re-isolated Strain No.	Plant from which Isolated	Condition of Plants at Termination of Experiment			Remarks
			Diseased	Dead	Healthy	
1	1a	No. 1	4**	0	0	All plants in this series showed symptoms of form I only. The four re-isolates similar in virulence to parent strain.
	1b	No. 1	4	0	0	
	1a-2	No. 2	4	0	0	
	1b-2	No. 2	2	0	2	
7	7a	No. 1	4	4	0	Symptoms in all diseased plants in the 7-series typical of form I. All these re-isolated strains except 7c are very virulent. Slight vascular invasion in the secondary roots only.
	7b	No. 1	4	4	0	
	7c	No. 1	0	0	4	
	7a-2	No. 2	4	0	0	
	7b-2	No. 2	4	0	0	
	7c-2	No. 2	4	0	0	
	7a-3	No. 3	4	4	0	Vascular penetration in the 7-3 series extends to tap root. Extremely virulent strains of form I.
	7b-3	No. 3	4	4	0	
	7c-3	No. 3	4	4	0	
11	11a	No. 1	4	4	0	All plants in this series showed symptoms of form I. Very virulent strains.
	11b	No. 1	4	4	0	
	11a-2	No. 2	4	4	0	
	11b-2	No. 2	4	4	0	
27	27a-1	No. 1	4	4	0	Plants show only symptoms of form II. Virulence almost equals that of 7-series.
	27a-2	No. 2	4	4	0	
	27a-3	No. 3	3	1	1	
	27b-3	No. 3	4	4	0	
32	32b	No. 1	4	0	0	Symptoms of form II only. Moderately virulent strains.
	32c	No. 1	4	0	0	
	32a-2	No. 2	3	0	1	
50	50a-2	No. 2	4	4	0	A very virulent strain which produces symptoms of form II.
Controls		May-June, 1933	0	0	8	
		Dec., 1933-Feb., 1934	0	0	8	

*The re-isolates of strains 1 and 7 were included in the May-June, 1933 experiment. All the others were in the Dec., 1933-Feb., 1934 tests.

**Only four plants were set in each can in these two tests.

The results of these experiments, as in many others of a similar nature, prove that the Fusaria cultured from diseased plants are the causal agents of Fusarium yellows. It is also proved that the integrity of each isolate is constant and that it produces only one form of the disease. In other experiments with the various strains of Fusaria isolated from plants showing symptoms of the two forms of yellows, this integrity has been as constant as any of the other characteristics of the pathogens. Despite repeated passage through susceptible plants of different varieties each strain continues to excite in the suscept symptoms which are specific for only one form of yellows.

Pathogenicity of California Isolates

The cultures of Fusarium isolated from the diseased celery plants obtained at Venice, Calif., in March 1934, have been tested several times for pathogenicity. The fungus has been re-isolated from plants infected in those tests, and the re-isolates have produced the same form of the disease as the parent strains. A typical example of the results of pathogenicity tests with these strains is afforded in the experiment of Nov. 28, 1934, in which three isolates were tested against plants of "Tall Golden" and Golden Phenomenal varieties.

TABLE 5. *Pathogenicity test of Fusaria isolated from discolored vascular tissue in roots of celery plants from Venice, Calif. Temperature 28° C.*

Isolate No.	Variety of Celery	Condition of Plants Mar. 1, 1935		
		Diseased	Dead	Healthy
53	"Tall Golden"	2	2	0
	Golden Phenomenal	2	2	0
54	"Tall Golden"	2	2	0
	Golden Phenomenal	1	0	1
55	"Tall Golden"	2	2	0
	Golden Phenomenal	1	0	1
Control	"Tall Golden"	0	0	2
	Golden Phenomenal	0	0	2

None of the infected plants in this test displayed any foliage symptoms and the leaves remained green until the wilting stage was reached. Isolate 53 was apparently more virulent than the others and this characteristic has been noted in other tests with these pathogens.

CLASSIFICATION[8]

GENERAL CONSIDERATIONS

The general characters of the pathogens concerned with Fusarium yellows as determined from their behavior in standard laboratory media indicate that they belong in the section Elegans of the genus Fusarium. The chief

[8]In the studies on the taxonomical phase of the yellows problem the senior author has had the assistance of Dr. C. D. Sherbakoff of the University of Tennessee. Dr. Sherbakoff made an intensive study at East Lansing in August 1934, of the isolates used in the taxonomical investigations. His suggestions and advice have expedited the classification of the celery yellows pathogens.

characters which show their relationship to this group are the types of micro- and macro-conidia produced, the presence of terminal and intercalary chlamydospores, and the color reactions. The absence of definite sporodochial structures aligns them with the members of the sub-section Orthocera, a group which includes such important pathogens as those which cause yellows of cabbage and sugar beet, and the wilts of flax, aster, and pea.

Difficulties in Classification of Fusaria

The difficulties encountered in classification studies with the celery pathogens, using recognized standard methods of procedure have been great, and are paralleled by similar experiences of many other investigators faced with the similar task of determining the relationship and name to be applied to a pathogenic Fusarium. They appear to be inherent in the present concepts of classification.

It is becoming increasingly clear that the ideals of classification as recommended by the Fusarium conference[9] held at Madison, Wis., in 1924 and attempted to be used by certain specialists, cannot have rigorous adherence if the needs of the situation are met. According to these recommendations, species and varieties must be distinguished by morphological characters only. The species include groups of individuals that can be distinguished by morphological characters and which must be "of such a nature as to be applicable and usable by mycologists in general and which will be most serviceable for practical purposes" (62, p. 843). The variety is distinguished by morphological characters of less importance than those used for specific segregation. Those groups of individuals differing from the species and variety only in certain physiological characters are separated as forms. It was the apparent intent of the framers of the nomenclatorial recommendations to devise a system which could be used to segregate species and varieties on the basis of morphological characters alone. This system was to be usable by mycologists in general and serviceable for practical purposes. It is extremely doubtful if this system is workable when applied to the separation of pathogenic and saprophytic Fusaria in the subsection Orthocera.

With full recognition of the monumental task undertaken by Wollenweber and his conspicuous success in bringing order out of the chaotic condition prevailing prior to the appearance of Appel and Wollenweber's monograph, it is pertinent to this discussion and as a justification for the procedure followed in classifying the celery Fusaria, to consider critically the results recently obtained by Wollenweber and his associates in the application of formal morphological criteria to the Elegans section of the genus which is of such extensive importance in phytopathology.

In Wollenweber's monograph (61) the section Elegans is subdivided into three groups which are separable on the basis of the presence and absence of sporodochia and by the comparative widths of the macroconidia, and in his latest treatment of the genus these subdivisions are continued (63). In the subsection Constrictum a number of Fusaria which formerly had specific names are made varieties or forms of *Fusarium bulbigenum*. *Fusarium lycopersici*, the tomato wilt pathogen, becomes *F. bulbigenum* f. 1, and it differs from *F. bulbigenum* in the absence of blue color in the stroma and in the host relationship. The watermelon wilt pathogen, *Fusarium niveum*, is made a variety of *F. bulbigenum*, and it is distinguished from the type by slightly broader conidia and the absence of a purple vinaceous color in the

[9] Those present at the conference were: H. W. Wollenweber, C. D. Sherbakoff, O. A. Reinking, Helen Johann, and Alice A. Bailey.

stroma. These appear mere name changes, following a rule with little or no gain unless one presupposes some phylogenetic advantage by stressing a connection with *F. bulbigenum*. In "Die Fusarien" by Wollenweber and Reinking, p. 107, the name of the tomato wilt pathogen has again been changed. In this latest treatment it now becomes *F. bulbigenum* v. *lycopersici*.

In the subsection Oxysporum similar changes have been made, evidently in an attempt to apply a formal rule for the sake of uniformity. The banana wilt pathogen, *Fusarium cubense*, is made a form of *Fusarium oxysporum*, from which it is distinguished by slight differences which sometimes occur in the length of the conidia, especially those produced in pionnotes, and by the parasitism on Musa. Hansford (17) has shown that this fungus is extremely variable morphologically. In his study of a large collection of isolates obtained from various substrata, he was unable to distinguish the pathogenic from the non-pathogenic forms by morphological criteria, sharply criticized the elaborate system of classification in use, and proposed stressing pathogenicity rather than exclusively morphology.

Further evidence of the difficulties in differentiating some of the parasitic Fusaria of the section Elegans by morphological and physiological characters is seen in the segregation of *F. oxysporum*, forms 3, 4, and 5. *F. oxysporum* f. 4 differs from f. 3 only in the absence of a benzolic odor in rice cultures. However, Hansford reports that some of his cultures of *F. cubense* (*F. oxysporum* f. 3) did not produce any benzolic aroma on rice. Furthermore, he states that some of the non-pathogenic cultures which were indistinguishable morphologically from the pathogenic ones did emit a strong benzolic odor when grown on this medium. Form 5 also produces no aroma on rice, and a comparison indicates that it differs from f. 3 and f. 4 only in host relationship. Apparently there are no significant differences among these three forms of *F. oxysporum*, and f. 5 can be differentiated only by inoculation into tobacco. It is also evident that there are saprophytic forms which are indistinguishable morphologically from the true pathogens and that the only method of differentiation is by infection tests. This situation is admitted by Reinking and Wollenweber, for in discussing the similarities of *F. oxysporum* f. 3 and *F. oxysporum* f. 5 they state (38, p. 195):

"The similarity of the organisms from a morphological standpoint indicates that there may be wild saprophytic soil forms of known pathogenic species. Because of the close relationship established for these two strains, it is evident that inoculation experiments are necessary to permit accurate differentiation of the wilt-producing organisms."

In discussing the relation between *F. cubense* and *F. oxysporum* var. *nicotianae*, Reinking and Wollenweber (38, p. 192) make the following statements:

"Experience has shown that such characters as slenderness, curvature, and state of normal conidia can only be relied upon under uniform conditions in so-called 'high-culture'. Slight differences in these characters may, however, occur in growing the fungus in single-spore cultures, both from one source and from different hosts or locations. Under such circumstances the fungus described here, as isolated from Honduras soil and identified as *F. oxysporum* var. *nicotianae*, may touch the border line or may be even a widespread saprophytic soil form of the banana wilt Fusarium, *F. cubense*. This saprophytic soil strain may have adapted itself to plants of economic importance, as Musa or other plants, gradually assuming parasitic habits. If this were so, *F. cubense* would include saprophytic and parasitic strains with or without odor, taxonomically speaking, in at least the following four forms:

"Form 1: Saprophytic form producing a benzolic odor.
"Form 2: Saprophytic form without odor.
"Form 3: Parasitic form with odor, cause of banana wilt.
"Form 4: Parasitic form without odor. (Synonym, *F. cubense* var. *inodoratum* Brandes.)

"This viewpoint touches a weak point in Fusarium taxonomy, as it reveals the difficulties encountered in separating border-line varieties from related species in the section Elegans. It is, therefore, only to be regarded as a working hypothesis, which possibly would lead to a considerable simplification of the system."

This illustration of the possibility of a single species of Fusarium existing in at least four forms which are indistinguishable morphologically emphasizes the futility of insistence upon classifying all pathogenic Fusaria by a strict morphological system.

The weakness of the morphological basis of classification is especially evident with respect to the members of the subsection Orthocera, whose identification on morphological characters alone presents unusual difficulties. These difficulties may in part be due to a lack of knowledge of the physiology of growth and reproduction of these Fusaria in artificial culture. This limitation of knowledge makes it difficult to decide whether or not the absence of a character is due to the genetical constitution of the fungus or to handicaps imposed by the conditions of artificial culture. There may be cited the failure of some isolates to produce sporodochia, pionnotes, or sclerotia, after prolonged cultivation in vitro and taxonomical work with such cultures would lead to inaccurate conclusions concerning the inherent capacity of the species to produce these structures.

Another difficulty is the necessity of obtaining conidia in the "normal" condition, since morphological comparisons are apparently of little value unless they are based on a study of macroconidia that are truly representative of the species. The condition of "Normkultur" is attainable with great difficulty in some species and apparently not at all in others. Thus, Linford (23) in his investigation of the pea wilt pathogen was unable to manipulate his cultures so that they produced a sufficient number of macroconidia for a taxonomic study. A similar difficulty is experienced with many other species and especially with those that do not produce sporodochia or pionnotes. The members of the subsection Orthocera are especially refractory in this respect and despite prolonged manipulation of the cultures, they rarely produce conidia that are suitable for taxonomic comparisons. This characteristic of the species in this group may be an inherent trait which is traceable to the mode of parasitism or it may be due to a baffling weakness in our technique of handling them in artificial cultures.

In the subsection Orthocera as treated in Wollenweber's monograph (61) and in the more recent work (63) it is apparent that the specific and varietal separation of the members of this group has been accomplished through a liberal interpretation of what constitutes distinct morphological differences. A comparison of the morphological characters in this group shows that it is impossible to separate the important members by this system unless minor differences are given exaggerated significance. The four chief members, *F. orthoceras*, *F. conglutinans*, *F. conglutinans* var. *callistephi*, and *Fusarium lini* show only slight differences in the dimensions of the macroconidia, and the value of this character in their diagnosis is questionable. This could be determined satisfactorily only by a statistical analysis of data from a study of cultures in a comparable condition. Furthermore, aside from parasitism, *F. conglutinans* differs from *F. orthoceras* mainly in the absence of color in the stroma, while morphological and physiological differences are not apparent in the separation of *F. conglutinans* and *F. conglutinans* var. *callistephi*.

In the writers' opinion, the concept that morphological differences are the only characteristics of Fusaria that should be recognized in taxonomic work, has resulted in an inflexible system of limited usefulness. A system of classifi-

cation that recognizes the value of morphological differences, but which utilizes other useful characters in demarcating species or varieties, appears to be needed definitely for Fusaria. The precedent established in the classification of bacteria may be cited as indicative of what may advantageously be done by use of pathogenicity and physiological criteria when morphological means of classification are lacking.

To phytopathologists the host relationship appears worthy of recognition in classifying the pathogenic forms of Fusarium. Apparently, however, it has not been accorded much consideration even though among certain groups this relationship is by far the most outstanding and differential character. In the subsection Orthocera, for example, parasitism readily separates the members of this group. Thus, *F. conglutinans* cannot be distinguished from its variety *callistephi* with certainty except by inoculation tests. The parasitic members of this subsection are not cross inoculable, and the specificity of the host relationship furnishes the most convincing evidence that they are not the same organism. Species demarcation could be accomplished by inoculation tests alone.

In the examples that have been cited there is enough evidence to reveal the weaknesses of the morphological system for the differentiation of some of the important parasitic species. Furthermore, the various criteria used for the differentiation of the members of the subsections Constrictum, Oxysporum, and Orthocera illustrate difficulties in the practical application of present rules of nomenclature. Rules that apply to one group of organisms will not necessarily work with another, and thus the segregation of species and varieties rests somewhat upon personal opinion. Analysis of the results that have been achieved through such use (personal opinion) tend to discourage attempts at identification and classification of parasitic forms of Fusarium (25).

If the present rules are adhered to in classifying the parasitic members of the subsection Orthocera, the only logical procedure would be to select the type species, which must be *F. lini* because of priority, and to make the other members either varieties or forms of this species. If the rules were followed strictly, the present known parasitic members of this subsection would become forms of *F. lini* and the classification would be as follows:

F. lini—cause of flax wilt.
F. lini—f. 1—cause of cabbage yellows. (Synonym *F. conglutinans.*)
F. lini—f. 2—cause of aster wilt. (Synonym *F. conglutinans* var. *callistephi*)
F. lini—f. 3—cause of beet wilt. (Synonym *F. conglutinans* var. *betae*)
F. lini—f. 4—cause of pea wilt. (Synonym *F. orthoceras* var. *pisi*)

While this classification is the only logical one if the recommendations and precedents of Wollenweber's classification are followed—namely, that of clearly recognizable morphological differences for segregation—it is apparent that this treatment involves drastic changes and would not in the least provide a practical, more convenient, or more workable classification. If the system now in use is not modified, the host relationship must be recognized as a character equal in importance to morphology, since it is only on the basis of parasitism that these fungi can be segregated specifically. If clearly recognizable and stable morphological differences are apparent in cultures that have been brought up to a condition of normal fructification, these char-

acters must be given proper consideration. If differential morphological characters are lacking, the host relationship offers a criterion for classification that is none the less significant. Of the parasitic species of Fusarium in the section Elegans none have a pronounced omnivorous habit. The parasitism of these fungi is restricted to closely related plants, usually to members of the same genus. The range of parasitism is so narrowly prescribed that practically all the species can be segregated by this characteristic. Since clearly defined morphological differences are often absent, a classification dependent primarily on this criterion is not the answer to the need for a practical and workable system.

FUSARIUM PATHOGENS OF CELERY

In the beginning of the taxonomic studies an attempt was made to identify the yellows pathogen on morphological grounds alone. At that time only one form of the disease had been distinguished, and the cultures used included only isolates from diseased plants grown in Michigan. By a study of the characteristics of the pathogen in pure cultures, it was possible to align the fungus with members of the *F. orthoceras* group, but no decision was reached as to the specific identity because the cultures did not produce normal macroconidia. Later, when two forms of the disease had been recognized and a collection of isolates obtained, a more intensive and extensive investigation was undertaken in an attempt to classify them by morphological characters. Still later, it became necessary to develop methods for segregating the two groups of isolates by means of other criteria.

Various media were tested in an attempt to find one that would stimulate the production of normal macroconidia, for it was evident early in the investigations that these pathogens were refractory in this respect. In all of the preliminary studies no isolates produced normal macroconidia in numbers sufficient for comparison with other species. In fact, the great majority of them formed only microconidia and chlamydospores. Various infusion agars were tested, including celery, oat, wheat, and potato, as well as those compounded of extracts of malt. A celery and a bean agar were made by extracting the juice from the petioles of celery and from the young pods of beans and sterilizing these liquids by filtration through Berkefeld candles and adding the clear and sterile filtrate to melted, plain agar in petri dishes. The results were the same with all media, the fungi failed to produce macroconidia after a series of transfers. No better results were obtained by using steamed slices of potato, celery, carrot, and other vegetable substrata. In the later studies, morphological and physiological characters were determined from the development of the isolates on four standard media, including an oat agar made by infusing below 60° F., 100 grams of ground oats in 1,000 cc. of water and adding to the strained infusion 2 per cent agar; and a potato agar made in the usual way and which contained 2 per cent agar and ½ per cent dextrose. Steamed rice was used for a study of color characters, and potato tuber plugs were utilized at various times for an investigation of sclerotial formation.

In only one culture have macroconidia been produced on the sterilized potato plugs or on other purely vegetable media. Macroconidia were eventually obtained in a small number of cultures by sub-culturing at three- to five-day intervals some especially responsive isolates for a period of about five months. Only a few of the cultures responded to this treatment, but they

were representative of the entire collection in all other characters. The responsive isolates included some only recently cultured as well as others that had been carried in stock for two to five years. The abundant formation of macroconidia in some of the cultures and the continued failure of others to respond to similar treatment is one of the idiosyncrasies of the pathogens obtained from plants affected with the two forms of the yellows disease.

The morphological and physiological characters of the Fusaria which cause form I and form II of yellows and which place these fungi in the subsection Orthocera of the section Elegans are as follows: the Fusaria are typical vascular parasites, which produce both terminal and intercalary, globose chlamydospores; the typically ovoid microconidia are not in chains, and the microconidia are usually greatly in excess; sclerotia are usually lacking but may occur occasionally in cultures of the pathogen causing form II of the disease; sporodochia do not occur, and pionnotes may or may not be present in cultures of the pathogen causing form I only (Pl. X: 3); on carbohydrate media the color, when present, is typical of the section, vinaceous to purplish vinaceous in the acid modification on rice and blue in the alkaline; the macroconidia are typically three-septate (Pl. XII: 1-4).

DIFFERENTIATION OF FORM I AND FORM II PATHOGENS

In the preliminary studies of the morphological characters of the pathogens which cause form I and form II of celery yellows, it was observed that no definite differences could be detected. Since macroconidia in numbers sufficient for diagnostic purposes had not been observed, and since it seemed likely that other criteria would have to be used in lieu of a biometrical analysis of the macroconidia, a search was made for other differential characteristics and other methods of analysis were tested. It was observed that on agar media and vegetable plugs the growth characteristics of the Fusaria which had been proved to cause two forms of the yellows disease were apparently similar, but on certain other media differences were noted which appeared to be of diagnostic value.

Differentiation by Color Reactions on Rice

The Fusarium yellows isolates were grown on various substrata to test for differential characters. None of these media except steamed rice was especially useful. On this medium the color reactions separated the isolates into two groups, one colored and the other colorless. When the cultures in each group were checked with the form of disease produced, it was found that those which were colorless on the rice were isolates of form II and the colored ones were those of form I. This color reaction was then used to type a collection of untested cultures and the differentiation of the two groups was checked by inoculation into susceptible varieties of celery. In all instances the cultures which formed color on the rice produced only form I of Fusarium yellows, while the colorless ones produced only form II. Subsequently, all isolates in the collection were subjected to this test and the color differentiation was specific for the two pathogens.

The range in color of the form I isolates on steamed rice is from pale vinaceous to spinel red in the acid modification and from rosalone purple to slate blue in the alkaline. In the dark, or in diffused light, the form II

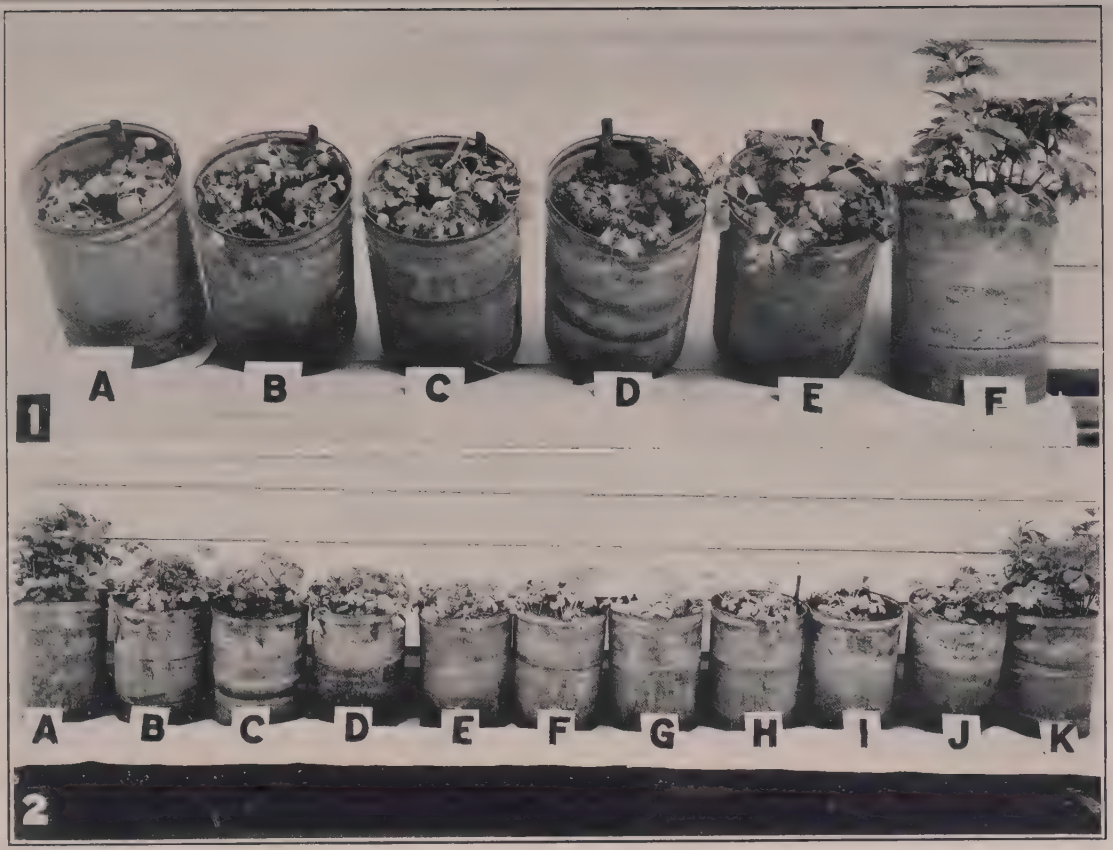

PLATE IX

1. Comparative virulence of Michigan, Ohio, and Colorado isolates of celery yellows pathogens. A—C, Michigan isolates 2, 3, and 101. D, isolate 17, Ohio. E, isolate 13, Colorado. F, check. Temperature 28° C. Period, January 28 to March 21, 1931. Tall strain, Golden Self-Blanching celery.

2. Variation in virulence of Michigan isolates of *Fusarium apii* and *F. apii* var. *pallidum*. A and K checks. B, G, H, and I, *F. apii*. C, D, E, F, and J, *F. apii* var. *pallidum*. Temperature 28° C. Period, March 18 to April 29, 1931. Tall strain, Golden Self-Blanching celery.

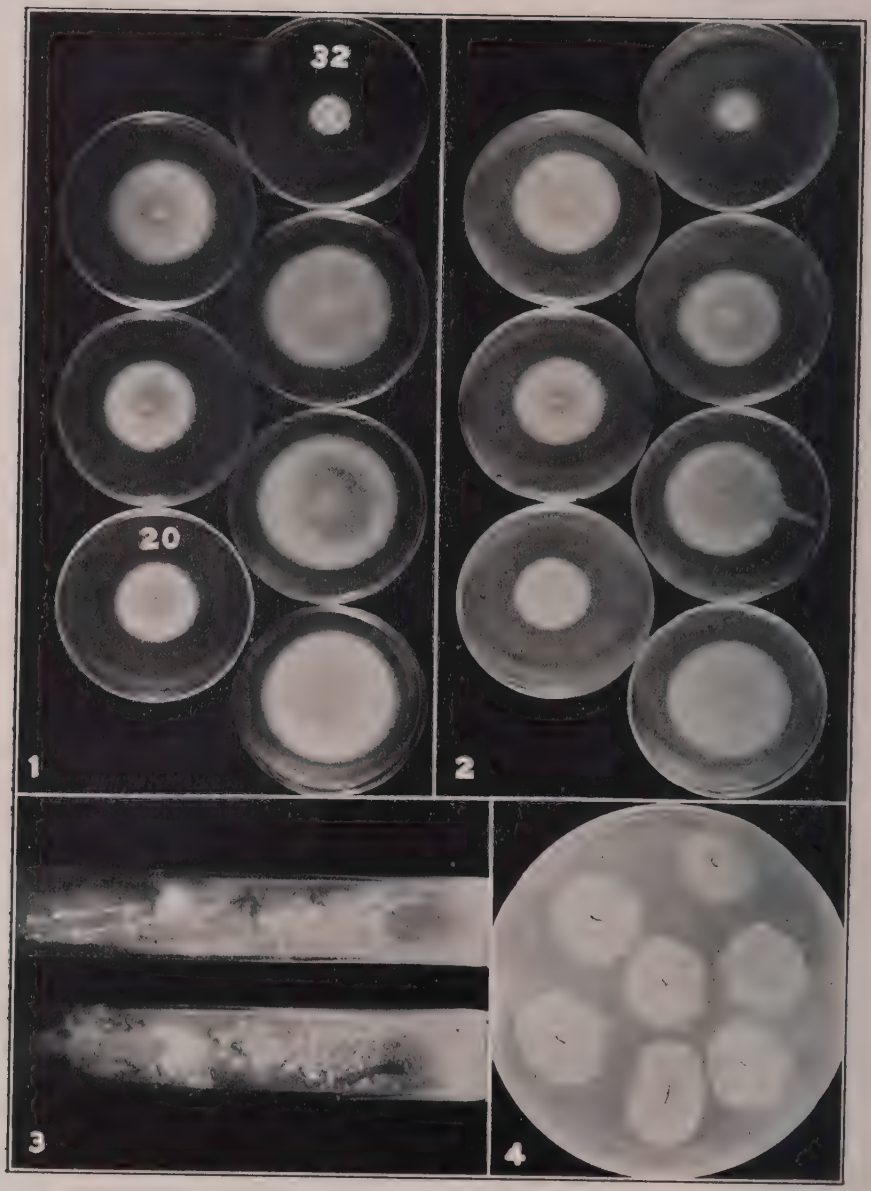

PLATE X

1-2. *Fusarium apii*, isolate 7 (1) and *F. apii* var. *pallidum*, isolate 3 (2) grown on synthetic agar for 136 hours at 20, 23, 24, 26, 28, 30, and 32° C. Maximum growth of *F. apii* occurred at 28 to 30° C., and of *F. apii* var. *pallidum* at 26 to 28° C.

3. Development of pionnotes in cultures of *F. apii*, isolates 88 and 86. Seventy-two hour cultures on potato hard agar containing ½ per cent dextrose.

4. Outgrowth of mycelium from bits of discolored vascular tissue taken from root of celery plant infected with *F. apii* var. *pallidum*. Prune agar medium.

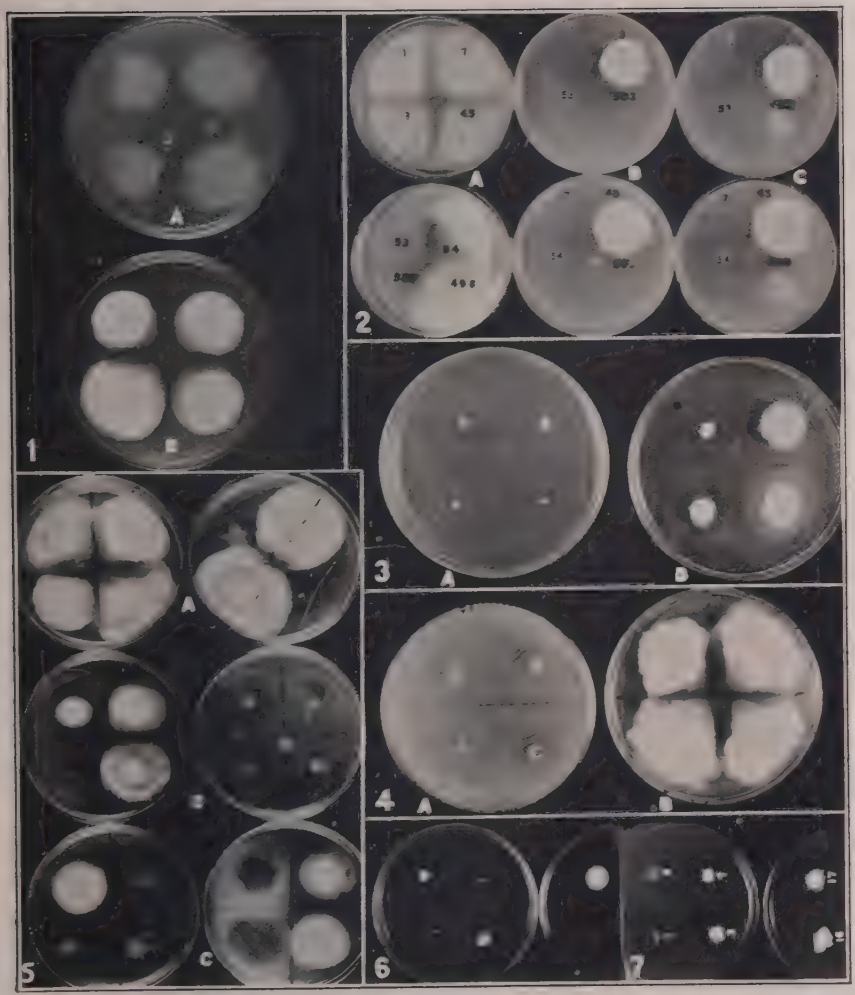

PLATE XI

1. *Fusarium apii* (A) and *F. apii* var. *pallidum* (B) grown 10 days at 25° C. on synthetic agar containing M/500 copper sulphate. A frondose margin and a Cinnamon Buff color of the mycelium distinguish *F. apii* from its variety with an even margin and a Cartridge Buff colony.

2. *Fusarium apii* (1 and 7); *F. apii* var. *pallidum* (3 and 45); *F. conglutinans* (496); *F. orthoceras*, celery strain, (503) and the Venice, California, pathogen (53 and 54), grown 10 days at 25° C. on synthetic agar containing M 300 copper sulphate (B and C) and on plain synthetic agar (A). The celery strain of *F. orthoceras* (503) is very intolerant of copper like *F. apii*. Other strains of this species react like *F. apii* var. *pallidum*. See table 9.

3. *Fusarium apii*, isolates 1, 7, 11, and 46 (A) grown 10 days on synthetic agar with M 300 copper sulphate and *F. apii* var. *pallidum* isolates 3, 26, 45, and 49 (B) with M/200 copper sulphate.

4. The same isolates as those in (3) grown 10 days on synthetic agar with M 300 copper chloride.

5. Differential toxic action of copper sulphate for classifying new isolates. Twenty four isolates grown on synthetic agar plus M/300 ($CuSO_4$). (A) Six are *F. apii* var. *pallidum* and two are *F. apii*. (B) five isolates are *F. apii* and three *F. apii* var. *pallidum*. (C) five isolates of *F. apii* and three of *F. apii* var. *pallidum*. Correctness of typing checked by inoculations on Golden Phenomenal celery.

6. Five isolates of *F. apii* and one of *F. apii* var. *pallidum* (lower left) grown 10 days on synthetic agar containing 1-100,000 malachite green. There is no differential toxic effect.

7. *Fusarium apii*, isolates 1, 7, and 17 and *F. apii* var. *pallidum*, isolates 2, 3, and 16 grown for 10 days on synthetic agar containing 1-4,444 crystal violet. Both pathogens are very tolerant of this dye.

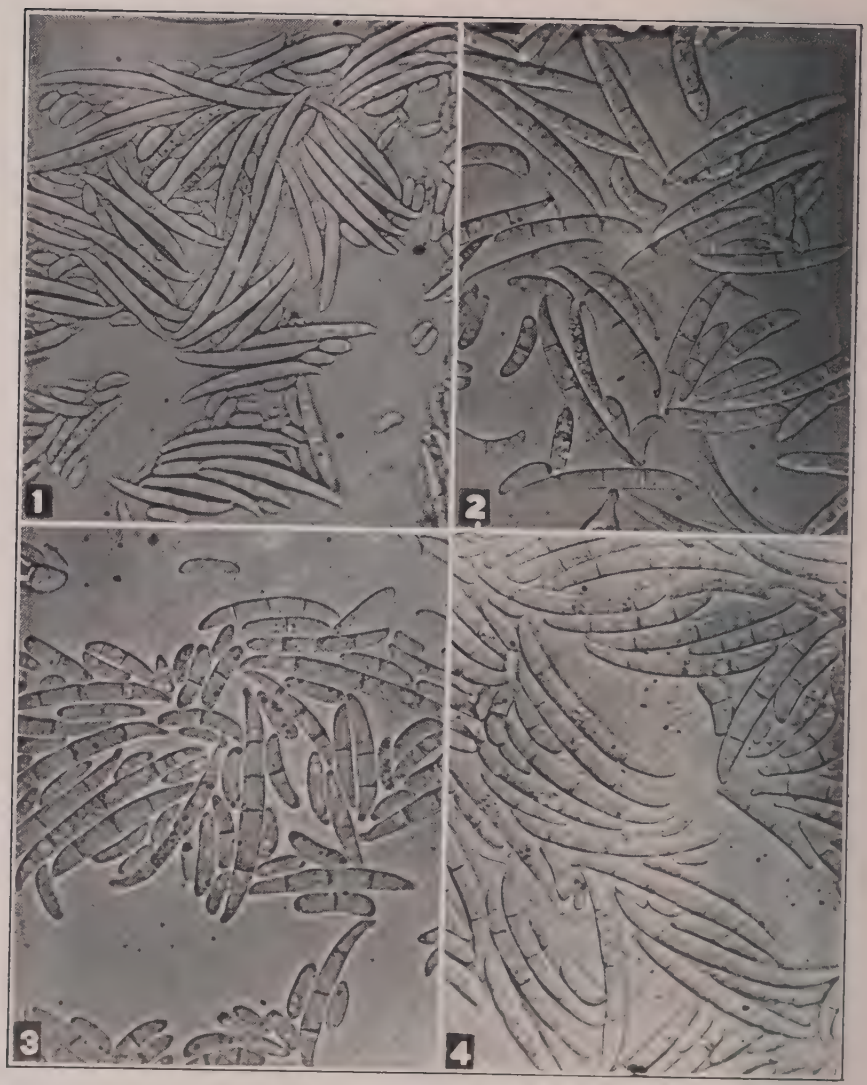

PLATE XII

1. Spores of *Fusarium apii*, isolate 64, from pionnotes in 12-day culture on potato hard agar containing one-half per cent dextrose. X 555.

2. Spores of *F. apii*, isolate 87, from pionnotes in 7-day culture on potato hard agar containing one-half per cent dextrose. X 792.

3-4. Spores of *F. apii* var. *pallidum*, isolate 81 (3) and isolate 82 (4) from 8-day cultures on oat hard agar. Photomicrographs of unstained spores, Eastman process plates, Wratten C filter. X 792.

TABLE 6. *Color reactions of Fusarium yellows pathogens and other Fusaria on steamed rice. Period of test, 10 weeks.*

Isolate No.	Disease Form	Color Reactions			
		After 3 Weeks		After 10 Weeks	
		Aerial Hyphae	Substratum	Aerial Hyphae	Submerged Hyphae and Substratum
1	I	Vinaceous	Spinel Red	Spinel Red	Rosalone Purple
7	I	Colorless	Vinaceous	Hydrange Pink	Rosalone Purple
8	I	Colorless	Spinel Red	Spinel Red	Rosalone Purple
10	I	Thulite Pink	Thulite Pink	Thulite Pink	Spinel Red
20	I	Pale Vinaceous	Deep Vinaceous	Pale Rose Purple	Spinel Red
46	I	Colorless	Purplish Vinaceous	Vinaceous	Dusky Slate Blue
3	II	Colorless	Colorless	Colorless	Colorless
26	II	Colorless	Colorless	Colorless	Colorless
45	II	Colorless	Colorless	Colorless	Colorless
40	II	Colorless	Colorless	Colorless	Colorless
49	II	Colorless	Colorless	Colorless	Colorless
F. conglutinans		Colorless	Colorless	Colorless	Colorless
F. conglutinans var. *callistephi*		Colorless	Colorless	Colorless	Colorless
F. orthoceras		Colorless	Vinaceous	Submerged (Vinaceous)	Indulan Blue

isolates are colorless, while under the same conditions those of form I are always colored. The typical reactions on rice of representative isolates of form I and form II and some related Fusaria are shown in Table 6.

The addition of comparatively large quantities of dextrose (2 to 5 per cent) to potato agar results in the production of color by the isolates of form I, but differentiation of the pathogens of Fusarium yellows on this medium is not so precise as on the rice. The selective action of certain toxic substances added to the culture medium has resulted in a sharper and more satisfactory separation.

Tests with Aniline Dyes

Representative isolates of the pathogens which cause form I and form II of yellows were grown on standard synthetic agar containing various concentrations of malachite green, brilliant green, and crystal violet, according to the method developed by Coons and Strong (10). The reactions of these isolates to the presence of these toxic substances in the culture medium were very similar to those of *F. orthoceras* and other members of the Orthocera subsection. Typical readings of these cultures are recorded in Table 7.

Among the various isolates only slight differences were noted in their reactions to the presence of the dyes in the agar. These differences were apparently of no significance, and the tabulated results indicate that the toxic effect of the dyes, as determined by the size of colony at the various concentrations, was much the same for all of the isolates tested. The isolates were all moderately sensitive to malachite green and very tolerant of the presence of crystal violet in the medium. Growth was usually stopped at about a concentration of 1:100,000 to 1:66,666 of malachite green (Pl. XI: 6), but it persisted to a 1:2,000 concentration of crystal violet (Pl. XI: 7). Brilliant green was not decolorized. The most outstanding characteristic of the isolates was their tolerance of crystal violet.

In comparing the reactions of these isolates with those of other parasitic members of the subsection Orthocera, it is evident that all are substantially

TABLE 7. *Reactions of celery Fusaria to various concentrations of aniline dyes in synthetic agar and to plain synthetic agar. Period 10 days. Temperature 25° C.*

Dye	Accession No.	Disease Form	1:400,000	1:200,000	1:100,000	1:66,666			Plain Synthetic Agar
Malachite Green.	1	I	*13.001	13.006	11.000	11.000			14.006
	7	I	13.001	13.001	11.000	11.006			14.001
	42	I	13.001	12.003	tr.	0			15.005
	3	II	13.003	12.004	11.006	11.000			15.007
	30	II	13.003	12.003	11.006	11.006			14.006
	40	II	13.003	12.003	11.006	tr.			14.000
			1:400,000	1:200,000	1:100,000	1:50,000			
Brilliant Green..	1	I	14.006	13.006	12.102	11.102			15.000
	7	I	13.001	13.001	12.001	0			15.000
	10	I	14.000	14.000	13.002	12.102			15.000
	3	II	14.003	13.003	13.002	12.001			15.000
	24	II	14.003	14.003	12.003	11.103			15.000
			1: 20,000	1: 10,000	1: 5,000	1: 3,000	1:2,000	1:1,000	
Crystal Violet...	1	I	12.001	12.001	12.001	11.001	11.000	tr.	15.000
	7	I	12.001	12.001	11.001	11.001	11.001	tr.	14.001
	42	I	12.001	12.001	12.001	12.001	12.001	tr.	14.000
	3	II	12.001	12.001	11.001	11.001	11.001	0	15.007
	30	II	11.001	11.001	12.002	12.002	11.001	0	15.001
	40	II	12.013	12.013	12.013	12.013	11.000	0	14.000

*The number scheme is that used by Coons and Strong (10) for recording readings of petri dish cultures. The values they used are as follows:

COLOR OF MYCELIUM

White	10
Red	20

BREADTH OF MYCELIAL MAT

No growth	0
Very slight growth	tr.
0.5 cm. to 1 cm.	1.
1 cm. to 2 cm.	2.
2 cm. to 3 cm.	3.
3 cm. to 4 cm.	4.
4 cm. to 5 cm.	5.

CHANGES IN MYCELIUM COLOR

No change	.0
Halo	.1
Strong decolorization	.2
Color intensified in mycelium	.3

EDGE OF COLONY

Even	.00
Ramose	.01
Frondose	.02

GROWTH FORM OF MYCELIUM

Submerged	.000
Cottony	.001
Villous	.002
Sericeous	.003
Tufted	.004
Submerged, cottony center	.005
Submerged, sericeous center	.006
Submerged, with cottony fringe at edge, atoll	.007
Wooly	.008

similar. Although *F. conglutinans* appears to be slightly more sensitive to malachite green than the celery pathogens, the differences are so slight that they can probably be accounted for by variations in judgment as to whether the reactions of the celery Fusaria place them in section 3 or section 4 of

the provisional key of groupings of the Fusaria (10, p. 10). The celery Fusaria are slightly more tolerant of crystal violet than *F. conglutinans* and *F. orthoceras* and decidedly tolerant in comparison with *F. lini*. The general reactions of the isolates, representing each form of the yellows disease, furnish additional evidence of their relationship to the group of parasites which belong to the Orthocera group, but these reactions are not of differential value for species diagnosis nor for classification with respect to the form of disease which they cause.

Reactions to Copper Salts

In some preliminary tests, Coons and Strong (10) found that copper sulphate added to the culture medium may be valuable in identifying some species of Fusarium, because *F. conglutinans* and *F. lycopersici* were found to tolerate the presence of copper sulphate in synthetic agar medium up to m/400 to m/300 concentrations.

Four representative isolates, which in the infection tests had caused form I of yellows and four which caused form II, were grown on synthetic agar to which was added amounts of m/10 copper sulphate to make a graded series of concentrations from m/1,000 to m/100.[10] Exactly 20 cc. of the agar was dispensed into each petri dish on a leveling stand. Four isolates were grown in each dish. The seeding of the center of each quadrant of the dish was done with a 1 mm. piece of No. 8 cotton thread taken from a potato agar slant on which the fungus had grown for ten days. The cultures were run in duplicate, and they were incubated for 10 days at 25° C. This test gave a sharp differentiation between the two groups of pathogens. The isolates of form I were more sensitive to the presence of the copper and, in addition, there were distinct differences in the shape and color of the thalli. Whereas all of the isolates of form I failed to produce a measurable growth on the agar containing copper sulphate at a concentration greater than m/300, those of form II still grew well at m/200. The mycelium of the form I isolates was submerged with a pronounced frondose margin, while the isolates of form II produced a distinctly cottony type of colony with an even margin (Pl. XI: 1). The mycelium of the isolates of form I was a cinnamon buff color in contrast to that of the isolates of form II, which was white. At the high concentrations, a strong precipitation took place, which formed an opaque halo around the edge of the colony of all isolates of form II. This was lacking around those of form I. Typical readings of the responses of those isolates to copper sulphate are given in Table 8.

In recording the characteristic reactions of these isolates by the number scheme used by Coons and Strong (10) (See footnote to table 7), a new character was encountered which necessitates an addition to their list. To each differential character which was used they assigned a numerical value for ease in recording descriptions. In this shorthand system a numerical value of 10 was given to those cultures with white mycelium and 20 to those with red. No other distinct color was noted. However, the mycelial

[10] In preparing the agar with a graded series of copper sulphate concentrations, m/10 copper sulphate was made by dissolving 25 gms. of c.p. copper sulphate in 1,000 cc. of distilled water. To obtain m/100 concentrations, m/10 copper sulphate was added in the proportion of 10 cc. to 90 cc. of synthetic agar; other concentrations were obtained by similar methods. When copper chloride was used a similar procedure was followed, m/10 stock solution being made by dissolving 17.05 gms. of c.p. copper chloride in 1,000 cc. of distilled water and adding measured portions of this solution to proportional quantities of synthetic agar to make the required dilution.

TABLE 8. *Responses of celery Fusaria to various concentrations of copper sulphate in synthetic agar and to plain synthetic agar.**

Accession No.	Isolate of Form	m/1,000 **	m/800	m/600	m/400	m/300	m/200	m/100	Synthetic Agar
1	I	33.020	33.020	33.020	31.020	31.020	tr.	0	15.000
7	I	33.020	34.020	33.020	33.020	32.020	tr.	0	15.000
10	I	32.020	33.020	32.020	32.020	30.020	tr.	0	15.000
46	I	34.020	34.020	34.020	32.020	32.020	tr.	0	15.000
3	II	15.005	14.001	13.001	13.001	13.001	12.101	0	15.001
26	II	15.005	15.001	14.001	14.001	12.001	11.001	0	15.001
45	II	15.001	15.001	13.001	14.001	13.001	12.101	0	15.000
49	II	15.001	14.001	14.001	14.001	13.001	12.101	0	15.000

*It is essential that 1.2 per cent agar be used, otherwise the readings will differ from those in this table. With larger quantities of agar, the toxicity of the medium will be decreased due to its increased adsorptive capacity for copper.

**Some of the readings above m/100 are omitted since the differential concentrations are between m/400 and m/100.

color of the celery isolates of form I was cinnamon buff on the plates containing copper salts. To the color characters previously enumerated by Coons and Strong it was necessary to add a third, -30- for brown mycelium in their system of notation.

A sharp differentiation between the two groups of isolates is effected by the use of copper sulphate in the agar and four characters have diagnostic value: (a) growth reaction; (b) form of mycelium; (c) color of mycelium; (d) edge of colony.

Still sharper differentiation was obtained by substituting copper chloride for copper sulphate (Pl. XI: 3). In general, the reactions of the isolates to cupric chloride in the agar were similar to those described for cupric sulphate, but the differential toxicity was a little greater and in addition there were other advantages in using the chloride salt. In the higher concentrations, when copper sulphate was added to the melted synthetic agar, a strong precipitation occurred which removed a portion of the copper from solution. A m/10 solution of each salt was made in distilled water, and accurately measured portions of hot, melted agar and the copper solution were mixed thoroughly and then dispensed into the petri dishes. Precipitation could usually be avoided by using the chloride instead of the sulphate salt and by adding the m/10 solution slowly to the boiling-hot agar.

In the tests with copper chloride, in addition to the celery pathogen, isolates of *F. conglutinans, F. conglutinans* var. *callistephi* and *F. orthoceras* were used for comparison. Typical records of the reactions of these pathogens and of the two groups of celery isolates are given in Table 9.

As shown in Table 8, the reactions of the celery isolates to copper sulphate permit clear-cut differentiation of the two groups. With copper chloride (Table 9) the cleavage was even more precise. It will be noted that the isolates of form I were much more sensitive to the copper salts than those of form II (Pl. XI: 2). The maximum colony diameter of the form I isolates on the m/500 concentration was one to two cm., whereas the isolates of form II grew as well as when on the plain synthetic agar. For the form II isolates there was no apparent toxic effect until the concentration of copper chloride was increased to m/200, a concentration at which all of the isolates of form I failed to produce any growth but where the thalli of form II were two to four cm. in diameter.

TABLE 9. *Reactions of celery Fusaria and F. conglutinans, F. conglutinans var. callistephi and F. orthoceras to various concentrations of copper chloride in synthetic agar and to plain synthetic agar. Period 10 days. Temperature 25° C.*

Accession No.	Isolate of Form	m/500	m/400	m/300	m/200	m/100	Synthetic Agar
1	I	32.020	32.020	31.020	tr.	0	15.000
7	I	32.020	32.020	31.020	tr.	0	15.000
10	I	32.020	32.020	31.020	tr.	0	15.000
46	I	33.020	32.020	31.020	tr.	0	14.000
3	II	15.005	15.005	15.005	12.005	tr.	14.000
26	II	15.005	15.005	14.005	13.005	tr.	14.000
45	II	15.005	15.005	15.005	13.005	tr.	14.000
49	II	15.005	15.005	15.005	14.005	tr.	15.000
496	*F. conglutinans*	34.005	34.020	33.020	31.020	31.020	14.000
497	*F. conglutinans* var. *callistephi*	16.007	15.007	15.001	13.001	tr.	14.005
498	*F. orthoceras*	15.005	14.005	14.001	12.001	tr.	14.000

Comparison tests, using *F. conglutinans*, showed that the growth characters of this organism were similar to those of the isolates of form I except that the tolerance of copper was far greater. The shape of the colony and the color of the mycelium conformed with those characteristics of the form I isolates, but the copper sensitiveness approximated more closely that of the form II pathogen. Just the reverse was true in the reactions of *F. orthoceras* and *F. conglutinans* var. *callistephi*.

The response of the celery pathogens to the presence of copper salts in the culture medium, when compared with the reactions of F. *conglutinans* and *F. orthoceras*, supplies additional evidence that these organisms form a related group. The color and form of the thallus of *F. conglutinans* and of the form I pathogen on synthetic agar, containing either copper sulphate or copper chloride, are strikingly similar, but the effect of the salts upon the growth rate is different. The form of the thallus and the color of the mycelium of *F. orthoceras* and of the form II pathogen are similar, and the tolerance of copper is about the same. Although these reactions indicate relationship among these fungi, the differential responses to inhibiting effects of the copper is suggestive of a specificity of reaction, comparable to their specificities in host relationships.

F. conglutinans var. *callistephi* has the same color of mycelium, but the edge of the colony differs, and the tolerance is much greater than that of the pathogen of form II. By obtaining the ratio of the diameter of the thallus on plain synthetic agar (1.2 per cent agar) to the diameter on this medium plus copper chloride, in, for example, m/300 concentration, the striking tolerance to copper of the form I pathogen as contrasted with the sensitiveness of the other Fusaria tested is shown. Since area of growth is concerned, the proportions judged in examining cultures are in fact as the squares of the ratios given. In the table cited the ratios are approximately as follows:

Form I pathogen	5.0
Form II pathogen	1.0
F. conglutinans	1.3
F. conglutinans var. *callistephi*	0.8
F. orthoceras (No. 498, 499)[11]	1.0

[11] *F. orthoceras* (accession 503 from celery) has shown the same color and copper toxicity reactions as *F. apii* but has not infected susceptible varieties of celery in our trials.

The comparative responses of the two celery pathogens to the presence of copper in the culture medium is additional evidence that these fungi are distinct.

Two simple tests are thus available for separation of the pathogens which cause the two forms of the yellows disease. The color reactions on rice give a very sharp differentiation and an equally satisfactory segregation can be obtained by growing the isolates on synthetic agar containing either copper sulphate or copper chloride. These reactions contribute strong support to the previous conclusion that there are two forms of the Fusarium yellows disease in Michigan distinguishable by the symptoms produced in infected plants.

Morphology

As stated elsewhere, it has not been possible to make a comparative morphological study of all the isolates obtained from plants affected with the two forms of the yellows disease, because the majority of these isolates failed to produce normal macroconidia in numbers sufficient for a taxonomical analysis. By sub-culturing on oat and potato hard agars at short intervals over a long period, certain responsive isolates have produced normal macroconidia and a biometrical analysis has been made of the spore types. Only seven isolates of the large number tested responded favorably to this treatment. Although it would be desirable to make a biometrical analysis of a larger number of the isolates, especially those cultured from plants grown in other states, there are no indications in the data obtained in these studies which suggest that it would alter the general results from the analysis of the smaller number. As shown elsewhere, the physiological reactions of the group of isolates which represent the two forms of yellows are consistently uniform. It is thus possible to segregate all of the isolates into two groups by culturing on rice. They are also easily separated by their responses to the presence of copper salts in the culture medium. The type of symptoms produced in the suscept is a third method which may be employed to classify untested strains.

For the study of spore types and other structures, the isolates selected were representative of the entire collection. These were sub-cultured at three- to five-day intervals on oat infusion hard agar or potato hard agar containing 0.5 per cent dextrose. The isolates of form II produced normal macroconidia only on the oat agar, while those of form I formed pionnotes and normal macroconidia only on the potato agar containing dextrose. As soon as the condition of "Normkultur" was attained—this required a minimum of three to five months—the spore measurements were made immediately from plain agar mounts prepared by a method suggested by Sherbakoff (42). A filar micrometer was used for all of the measurements and at a magnification of approximately 800 with a Leitz 3 mm. apochromatic objective. The spore mounts of form I were made from pionnotes, but since form II did not produce these structures, the spores were intermingled with mycelium. The data given on spore sizes are the means of the dimensions of 25 to 50 typical spores of each kind that occurred in the cultures. Of these isolates some produced spores of a certain type in such small numbers that it was impossible to measure the minimum number. For example, the two-septate spores, occurred very sparsely in the cultures of the form II pathogen, while most of the strains produced few or none of the four-to-five septate macroconidia. The typical three-septate macroconidia were present

in large numbers when the measurements were made. The 0-septate spores were nearly always in excess of all other types.

The mean and range of the spore sizes, in microns, of the seven isolates are as follows:

Form I	Isolate No. 7		Mean	Range
	0 — septate		9.0 x 3.1	(6.3 — 13.8 x 1.7 — 4.5)
	1 — "		17.9 x 3.8	(13.8 — 23.7 x 3.4 — 4.3)
	2 — "	rare	22.5 x 3.9	(20.0 — 27.6 x 3.6 — 4.1)
	3 — "		41.4 x 4.3	(28.9 — 53.8 x 3.1 — 4.7)
	4 — "	very rare	46.0 x 4.1	(41.4 — 51.0 x 3.8 — 4.4)
	5 — "	" "	48.3 x 4.8	
	6 — "	0		
	Chlamydospores		9.2 x 7.8	(6.2 — 13.8 x 5.8 — 9.8)
	Isolate No. 64			
	0 — septate		9.2 x 3.0	(4.8 — 13.8 x 2.0 — 3.8)
	1 — "		18.8 x 3.8	(12.9 — 25.9 x 3.0 — 4.5)
	2 — "	rare	25.5 x 4.1	(21.6 — 28.6 x 3.8 — 4.2)
	3 — "		37.7 x 4.2	(27.6 — 45.3 x 3.4 — 4.8)
	4 — "	very rare	42.0 x 4.4	(41.4 — 43.6 x 4.0 — 4.8)
	5 — "	0		
	6 — "	0		
	Chlamydospores		9.1 x 8.0	(6.9 — 12.4 x 6.9 — 9.6)
	Isolate No. 87			
	0 — septate		10.1 x 3.4	(6.3 — 13.8 x 2.4 — 4.7)
	1 — "		19.0 x 4.0	(13.8 — 25.2 x 2.1 — 4.8)
	2 — "	rare	23.9 x 4.5	(21.7 — 30.3 x 3.3 — 5.4)
	3 — "		37.0 x 4.5	(30.4 — 49.7 x 3.5 — 5.5)
	4 — "	rare	46.0 x 4.9	(41.4 — 52.8 x 4.6 — 5.5)
	5 — "	"	46.5 x 4.9	(43.5 — 53.1 x 4.5 — 5.5)
	6 — "	0		
	Chlamydospores		9.0 x 8.3	(7.7 — 10.9 x 6.9 —10.9)
Form II	Isolate No. 3			
	0 — septate		11.7 x 3.7	(8.5 — 16.8 x 2.5 — 4.8)
	1 — "		17.4 x 4.0	(12.0 — 20.7 x 3.5 — 4.6)
	2 — "		20.0 x 4.1	(22.1 — 37.9 x 3.4 — 4.9)
	3 — "		41.4 x 4.2	(31.0 — 55.2 x 3.6 — 4.8)
	4 — "	rare	47.0 x 4.3	(41.4 — 55.5 x 3.5 — 5.4)
	5 — "	0		
	6 — "	very rare	56.6 x 4.5	
	Chlamydospores		9.0 x 7.6	(5.5 — 12.4 x 5.4 — 9.9)
	Isolate No. 49			
	0 — septate		9.0 x 3.1	(6.3 — 13.8 x 1.7 — 4.5)
	1 — "		18.6 x 3.9	(11.0 — 26.0 x 3.6 — 4.5)
	2 — "	rare	22.7 x 3.7	(15.9 — 28.3 x 3.0 — 4.1)
	3 — "		38.3 x 4.1	(27.6 — 48.3 x 3.6 — 4.9)
	4 — "	rare	47.7 x 4.4	(42.4 — 53.1 x 4.1 — 5.0)
	5 — "	very rare	47.0 x 4.6	(45.5 — 48.3 x 4.3 — 5.0)
	6 — "	0		
	Chlamydospores		9.0 x 5.9	(7.2 — 11.8 x 6.9 —11.0)
	Isolate No. 80			
	0 — septate		9.6 x 3.3	(6.9 — 13.8 x 2.5 — 4.7)
	1 — "		16.2 x 4.1	(12.5 — 23.6 x 3.1 — 5.2)
	2 — "		22.0 x 4.4	(17.7 — 26.0 x 3.4 — 5.1)
	3 — "		40.7 x 4.4	(24.3 — 49.0 x 3.6 — 5.0)
	4 — "		46.2 x 4.9	(39.3 — 56.4 x 4.2 — 5.5)
	5 — "		51.0 x 5.1	(43.9 — 55.2 x 4.8 — 5.6)
	6 — "	0		
	Chlamydospores		7.9 x 7.7	(6.2 — 11.6 x 5.9 —10.4)
	Isolate No. 81			
	0 — septate		9.0 x 3.8	(5.8 — 15.3 x 2.0 — 4.8)
	1 — "		16.3 x 4.0	(12.6 — 20.7 x 3.2 — 4.6)
	2 — "		19.3 x 3.9	(16.0 — 22.6 x 3.2 — 4.7)
	3 — "		37.3 x 4.3	(27.6 — 51.0 x 3.4 — 5.3)
	4 — "	rare	41.5 x 4.3	(37.8 — 44.7 x 3.9 — 4.6)
	5 — "	very rare	45.2 x 4.2	(36.9 — 51.7 x 4.0 — 4.7)
	6 — "	0		
	Chlamydospores		8.7 x 8.0	(6.2 — 11.5 x 6.0 —10.7)

The data on the spore measurements of the two groups of isolates were subjected to statistical analysis to determine whether there were any significant differences in the spore sizes. In this analysis the dimensions of 100 to 135 of the 0-, one-, and three-septate conidia and of the chlamydospores were used, but on account of their comparative rarity it was necessary to use a smaller number of the two- and four- septate spores and the five-septate conidia were not included because of their rare occurrence in the cultures. The standard deviation of each spore type was calculated for the two groups and then compared for significant differences. None was noted except that the one-septate spores of isolates of form II are shorter than those of form I. The mean of the spore sizes and the probable errors as determined by this method are as follows:

	Isolates of Form I	Isolates of Form II
0 — septate	10.30 ± 0.14 x 3.42 ± 0.03 μ	10.0 ± 0.11 x 3.43 ± 0.03 μ
1 — "	18.63 ± 0.02 x 3.91 ± 0.11 μ	16.87 ± 0.02 x 4.07 ± 0.002μ
2 — "	24.15 ± 0.39 x 4.29 ± 0.006μ	22.40 ± 0.45 x 4.18 ± 0.017μ
3 — "	39.05 ± 0.26 x 4.29 ± 0.02 μ	39.33 ± 0.43 x 4.29 ± 0.03 μ
4 — "	45.74 ± 0.43 x 4.69 ± 0.01 μ	45.81 ± 0.26 x 4.62 ± 0.04 μ
5 — "	46.6 x 4.83 μ	48.30 x 4.83 μ
Chlamydospores	8.62 ± 0.09 x 7.86 ± 0.08 μ	8.49 ± 0.09 x 8.10 ± 0.06 μ

This analysis shows that, in general, there is so little difference in the spore sizes of the two celery pathogens that if they are compared on this basis alone they could not be distinguished accurately. Differences in gross morphology, physiology, and host responses show clearly, however, that they are not identical. In fact the differences between these two pathogens are as great or greater than those which have been used in the specific segregation of *F. conglutinans* and *F. orthoceras*. Because of their morphological similarities, these pathogens are best considered as belonging to one species. Gross morphological differences, which include pionnotal and sclerotial production, together with distinct physiological reactions and host relationships justify a varietal separation.

In comparing spore dimensions, especially of the three-septate conidia—which are the most typical and significant ones—with those of other members of the subsection Orthocera, it is evident that there are marked differences in breadth. Since spore variability is much greater in the long diameter, the comparative widths are considered a more valuable criterion for taxonomic purposes. Both *F. conglutinans* and *F. orthoceras* have much narrower spores than the celery pathogens. If these are real differences the celery pathogens are morphologically distinct from these species in the Orthocera group and merit a specific ranking on this basis.

If it were possible to obtain spore dimensions of *F. conglutinans, F. orthoceras,* and other members of the Orthocera group, from cultures in a condition comparable to that attained in some of the isolates of the celery pathogens, they would be valuable for comparative purposes. The suppression of some characters by the conditions of artificial culture increases the difficulties of classification and makes the collection of suitable data dependent upon the selection of favorable substrata and of particular manipulations needed to stimulate normal spore production in each species. A comparative study of all members of the Orthocera subsection in this normal condition would aid in clarifying the problem of inter-relationship among these

fungi. Until such a study is made, the question as to whether the differences in spore dimensions of the celery pathogens and of other members of this group are real or due to variations in conditions of the cultures cannot be answered.

The authors believe that the celery pathogens differ sufficiently from other members of the Orthocera group to constitute a new species. The most important differential character is the distinct host relationship and it is chiefly on this basis that the segregation is made. The morphological characters, as determined in these studies, apparently are distinct enough to warrant this classification, but it is preferable to leave this question in abeyance until a more equitable spore comparison can be made with other members of the subsection. Since the fungus which causes form I of the yellows disease was isolated first and was studied for a number of years before the form II pathogen was cultured, it is made the type species, *Fusarium apii*, n. sp. The form II pathogen is distinguished from *F. apii* by its gross morphological characters and distinct physiological reactions, and is made a variety of the type species. The trinomial *Fusarium apii* var. *pallidum*, n. var., is proposed for this pathogen. The technical descriptions of these fungi are as follows:

Fusarium apii Nelson and Sherbakoff, n. sp.[12]

SYNONYM—*Fusarium apii* Nelson and Cochran, *nomen nudum*.
Fusarium orthoceras var. *apii* Wollenweber and Reinking.

Mycelium white, on rice aerial or submerged, the aerial hyphae at first colorless, typically becoming Pale Vinaceous to Rosalone Purple; submerged hyphae and substratum Pale Vinaceous to Spinel Red, sometimes becoming Slate Blue. No sporodochia; conidia occasionally in discrete, creamy pionnotes. Microconidia always in excess; 0- and 1-septate abundant, the 2-septate usually rare. Macroconidia typically 3-septate, cylindrical to curved, slightly pedicellate, gradually attenuated toward the ends, the apical cell typically abruptly curved. 0-septate mean, 10 x 3.4 μ, mostly 8.3 — 13.0 x 3.1 — 3.8 (extremes, 4.8 — 15.4 x 2.0 — 4.7); 1-septate, 18.6 x 3.9, mostly 14.5 — 21.4 x 3.5 — 4.3 (12.9 — 25.9 x 2.1 — 4.8); 2-septate, rare, 24.1 x 4.3, mostly 21.4 — 27.0 x 3.7 — 4.3 (20.0 — 30.3 x 3.3 — 5.4); 3-septate, 39.0 x 4.3, mostly 34.5 — 40.7 x 3.9 — 4.5 (27.6 — 53.8 x 3.1 — 5.5); 4-septate, rare, 45.7 x 4.7, mostly 42.8 — 48.0 x 4.5 — 5.0 (41.4 — 52.8 x 3.8 — 5.5); 5-septate, very rare, 46.7 x 4.8 (43.5 — 53.1 x 4.5 — 5.5). Chlamydospores terminal, intercalary or intraconidial, subglobose to pyriform, smooth, singly or in chains of twos, 8.6 x 7.9 μ. No sclerotia. Moderately sensitive to malachite green, growth limit about 1-100,000 to 1-66,666; very tolerant of crystal violet, growth to about 1-1,500; brilliant green not decolorized; moderately tolerant of copper salts, growth to about m/300 copper sulphate or copper chloride in standard synthetic agar. On standard synthetic agar containing copper salts, mycelium typically submerged, Cinnamon Buff; edge of thallus frondose. Coefficient of copper toxicity at m/300 = 5.0. Optimum temperature 28-29° C. Parasitic in tracheae of roots, crowns, petioles and leaflets of *Apium graveolens* var. *dulce*. Cause of Fusarium yellows of celery, form I, in United States and Canada.

Fusarium apii var. *pallidum* Nelson and Sherbakoff, n. var.

SYNONYM—*Fusarium apii* var. *pallidum* Nelson and Cochran, *nomen nudum*.
Fusarium orthoceras var. *apii* f. 1 Wollenweber and Reinking.

Mycelium and substratum always colorless. Conidia produced singly or in false heads, not in sporodochia or in pionnotes. Microconidia always in excess, 0-, 1-, and 2-septate

[12]The two Fusaria described here were referred to, without description, under the names herein proposed in a paper presented by Nelson and Cochran (31) at the Pittsburgh meeting of the American Phytopathological Society, December 1934.

usually abundant. 0-septate mean, 10.0 x 3.4 μ, mostly 6.9 — 12.1 x 3.1 — 4.1 (extremes 5.8 — 16.8 x 2.0 — 4.8); 1-septate, 16.9 x 4.0, mostly 12.1 — 19.3 x 3.6 — 4.4 (11.0 — 26.0 x 3.0 — 5.2); 2-septate, 22.4 x 4.2, mostly 17.9 — 34.1 x 3.8 — 4.6 (15.9 — 37.9 x 3.0 — 5.1). Macroconidia typically 3-septate, 39.3 x 4.3, mostly 34.5 — 40.7 x 3.9 — 4.7 (24.3 — 51.0 x 3.4 — 5.3); 4-septate, rare, 45.8 x 4.6, mostly 42.1 — 48.3 x 4.2 — 5.0 (31.0 — 55.2 x 3.6 — 5.5); 5-septate, very rare, 48.3 x 4.8 (36.9 — 55.2 x 4.0 — 5.6); 6-septate, extremely rare, 56.7 x 4.5. Chlamydospores 8.5 x 8.1 μ. Sclerotia rare, blue. Reactions to malachite green, crystal violet, and brilliant green like those of *F. apii*. Very tolerant of copper salts, growth to about m/100 copper sulphate or copper chloride in standard synthetic agar. Coefficient of copper toxicity at m/300 = 1.0. On standard synthetic agar containing copper salts, mycelium typically aerial, white; edge of thallus even. Optimum temperature, 26-28° C. Parasitic in tracheae of roots, crowns, petioles, and leaflets of *Apium graveolens* var. *dulce*. Cause of Fusarium yellows of celery, form II, in United States and Canada.

Latin Description

Fusarium apii Nelson et Sherbakoff, sp. nov.

Synonym—*Fusarium apii* Nelson et Cochran, *nomen nudum*.
Fusarium orthoceras var. *apii* Wollenweber et Reinking.

Mycelio albo, ad pultem oryzinam aerio vel immerso, hyphis aeriis ex albis pallide vinaceis vel purpureis "Rosalone", hyphis immersis (et ipso substrato) pallide vinaceis vel rubris "Spinel", interdum coeruleis ("Slate-Blue"), sporodochiis nullis; conidiis unicis vel in capitulis falsis e conidiophoris simplicibus, non ramosis, raro in discreto cremeo pionnote dispositis; microconidiis semper numerosioribus, 0-septatis et 1-septatis vulgo abundantibus, 2-septatis vulgo raris, macroconidiis vulgo paucioribus, typice 3-septatis, cylindricis vel curvulis, sub-pedicellatis, ad apiceum et basim gradatim attenuatis, cellula apicale typice abrupto curva; sporis 0-septatis ovoideis, 1- et 2-septatis ovoideis vel curvulis; 0-septatis in medio 10 x 3.4 μ, plerumque 8.3 — 13 x 3.1 —3.8 (extremis 4.8 — 15.4 x 2.0 — 4.7); 1-septatis, 18.6 x 3.9, plerumque 14.5 — 21.4 x 3.5 — 4.3 (12.9 — 25.9 x 2.1 — 4.8); 2-septatis, raris, 24.1 x 4.3, plerumque 21.4 — 27.0 x 3.7 — 4.3 (20.0 — 30.3 x 3.3 — 5.4); 3-septatis, 39.0 x 4.3, plerumque 34.5 —40.7 x 3.9 — 4.5 (27.6 — 53.8 x 3.1 — 5.5); 4-septatis, raris, 45.7 x 4.7, plerumque 42.8 — 48.0 x 4.5 — 5.0 (41.4 — 52.8 x 3.8 — 5.5); 5-septatis, multo rarioribus, 46.7 x 4.8 (43.5 — 53.1 x 4.5 — 5.5); chlamydosporis terminalibus vel intercalaribus in hyphis et intercalaribus in conidiis, subglobosis vel piriformibus, glabris, singulis vel binis, 8.6 x 7.9 μ; sclerotiis nullis. Species parasitica, tracheas habitans, in radicibus, caule, petiolis et foliolis *Apii graveolentis* var. *dulcis*. Efficit morbum dictum "Fusarium yellows of celery", formam primam, in America boreale.

Fusarium apii var. *pallidum* Nelson et Sherbakoff, var. nov.

Synonym—*Fusarium apii* var. *pallidum* Nelson et Cochran, *nomen nudum*.
Fusarium orthoceras var. *apii* f. 1 Wollenweber et Reinking.

Mycelio et substrato semper incoloratis; conidiis unicis vel in capitulis falsis, pionnote et sporodochiis nullis; microconidiis semper numerosioribus, 0-septatis, 1-septatis et 2-septatis vulgo abundantibus; 0-septatis in medio 10.0 x 3.4 μ, plerumque 6.9 — 12.1 x 3.1 — 4.1 (extremis 5.8 — 16.8 x 2.0 — 4.8); 1-septatis, 16.9 x 4.0, plerumque 12.1 — 19.3 x 3.6 — 4.4 (11.0 — 26.0 x 3.0 — 5.2); 2-septatis, 22.4 x 4.2, plerumque, 17.9 — 34.1 x 3.8 — 4.6 (15.9 — 37.9 x 3.0 — 5.1); macroconidiis typice 3-septatis 39.3 x 4.3, plerumque, 34.5 — 40.7 x 3.9 — 4.7 (24.3 — 51.0 x 3.4 — 5.3); 4-septatis, raris, 45.8 x 4.6, plerumque 42.1 — 48.3 x 4.2 — 5.0 (31.0 — 55.2 x 3.6 — 5.5); 5-septatis, rarioribus, 48.3 x 4.8 (36.9 — 55.2 x 4.0 — 5.6); 6-septatis, rarissimis, 56.7 x 4.5; chlamydosporis, 8.5 x 8.1 μ, sclerotiis raris, coeruliis. Species parasitica, tracheas habitans, in radicibus, caule, petiolis et foliolis *Apii graveolentis* var. *dulcis*. Efficit morbum dictum "Fusarium yellows of celery", formam secundam, in America boreale.

ENVIRONMENTAL RELATIONS OF FUSARIUM YELLOWS OF CELERY

INFLUENCE OF TEMPERATURE ON GROWTH RATE OF *F. APII* AND *F. APII* VAR. *PALLIDUM*

The most rapid radial enlargement of the thalli of parasitic members of the subsection Orthocera occurs within a rather narrow range and the mycelial development is greatest at 26-30° C. In general, diseases caused by these Fusaria develop most rapidly at temperatures which approach the optimum for growth of the pathogen. Pea wilt is an exception, however, for it attacks the pea plant most actively at about 22° C., while the optimum for the pathogen is 27-30° C. The optimum soil temperature for infection of susceptible varieties of cabbage by *F. conglutinans* is also lower than the optimum temperature for the growth of the fungus. It is noteworthy that both pea and cabbage are more susceptible to infection when grown at soil temperatures that stimulate their most rapid development. Flax wilt, however, develops more actively at soil temperatures higher than the optimum for development of the flax plant. The influence of differential temperatures upon the development of *Fusarium apii* and *F. apii* var. *pallidum* has been given considerable attention as a prelude to the studies upon the relation of soil temperatures to the occurrence of celery yellows.

Gardner (15) studied the relation of temperatures to the growth of the Fusarium which he isolated from celery plants in Indiana and found that the organism made practically no growth at 10 and 35° C. and grew best at 25 to 27° C. Wilson states (58) that the optimum temperature for the growth of the fungus which he isolated from affected plants in Ohio is nearer 30° C. than 25° C., and Ryker (40) in his studies at Wisconsin lists the optimum as close to 28° C., the minimum at slightly below 8° C., and the maximum above 36° C.

Preliminary studies in 1920 indicated that the pathogen now identified as *Fusarium apii* made the most rapid growth at about 28° C. In this determination a small differential thermostat—a modification of the Genong type—was used. Later a much larger thermostat with 10 compartments and constructed so as to maintain temperatures with considerably less fluctuation was utilized to determine the approximate minimum, optimum, and maximum thermal limits for growth of both *Fusarium apii* and *F. apii* var. *pallidum*. In these tests five isolates were used, three of *F. apii* and two of *F. apii* var. *pallidum*. In preparing the petri dish cultures for exposure to the differential temperatures the method previously described for seeding the dye and copper media in the taxonomic studies was followed. Twenty cc. of the plain synthetic agar was dispensed into each dish, and duplicate cultures were placed in each of the 10 chambers of the thermostat and in two electric incubators which were used to extend the range of the higher temperatures. Morning and evening records were taken daily of the temperature in each compartment. There was considerable temperature variation in some of the compartments, especially in those at the ends. Temperature range in each chamber of the thermostat and in the two electric incubators, and the mean diameters of the two thalli of each of the isolates are given in Table 10.

TABLE 10. *Growth responses on synthetic agar of F. apii and F. apii var. pallidum to various temperatures. Incubation period 120 hours.*

Temperature, ° C.	Mean Diameter in cms. of Two Thalli of					Mean Diameter of All Thalli cms.
	F. apii			*F. apii* var. *pallidum*		
	Isolate No.			Isolate No.		
	1	7	21	13	17	
10.0—12.0	0.8	0.0	0.1	0.0	0.0	0.18
12.5—14.5	1.4	1.1	0.2	—**	0.3	0.6
14.0—16.5	2.0	1.5	0.8	1.2	0.9	1.3
16.5—18.5	2.1	2.3	1.8	2.0	1.0	1.8
17.5 -19.5	1.7*	2.5	2.7	2.3	1.9	2.4
18.5—20.5	2.7	3.2	3.0	2.4	2.4	2.7
19.5—21.5	2.8	2.0	2.3*	2.5	1.5	2.2
21.0—23.0	3.5	3.6	2.8	3.1	2.5	3.1
22.0—24.0	4.7	4.5	3.5	3.4	3.0	3.8
26.0 27.5	5.5	4.5	5.5	5.0	3.7	4.8
***27.5—28.5	6.0	5.5	6.0	6.1	6.0	5.9
***31.5—32.5	0.2	0.2	0.0	0.0	1.2	0.4

*Measurement of one thallus, no growth in duplicate culture.
**Contaminating fungus vitiated reading.
***Electric incubator.

The results of this test show the approximate minimum, optimum, and maximum temperatures for growth of representative isolates of the pathogens which cause the two forms of celery yellows. Undoubtedly some of the variations in the readings among the cultures may be attributed to the limitations of accuracy in the equipment used. It is believed that the average for all cultures gives a fair picture of behavior to be expected from those pathogens in their reaction to temperature. The maximum growth of all isolates occured at approximately 28° C., and the minimum was at 10° C. There was but scant growth at 32.5° C., and the maximum temperature is slightly above this.

The record obtained with the Genong thermostat were useful in determining the approximate maximum and minimum temperatures for the growth of *F. apii* and *F. apii* var. *pallidum,* but the optimal temperatures were not clearly defined for no cultures were grown in the range from 28 to 32° C. For a more accurate determination of the optimum temperature requirements of these pathogens it was necessary to utilize other equipment.

DeKhotinsky incubators were used for further studies on the relation of temperature to mycelial development. In these incubators the temperatures were controlled within limits of ± 0.25 C. In the first test two isolates each of *F. apii* and *F. apii* var. *pallidum* were grown for 112 hours, at 22, 24, 26, 28 and 30° C. In the second test only one isolate of each pathogen was used and the period of exposure was 136 hours at temperatures ranging by 2-degree steps from 20 to 32° C. The conditions were similar in each test. The responses of these isolates to the differential temperatures are summarized in Table 11.

TABLE 11. *The relation of temperature to mycelial development of F. apii and F. apii var. pallidum.*

Pathogen	Period	Mean Diameter in cms. of Two Thalli in Petri Dish Cultures on Synthetic Agar at a Temperature of:						
		20° C.	22° C.	24° C.	26° C.	28° C.	30° C.	32° C.
F. apii								
Isolate 1	112 hrs.	.....	4.1	5.0	5.9	6.1	5.5	
" 7	112 "	.....	3.7	4.2	5.0	5.6	5.6	
" 7	136 "	3.8	4.5	5.3	6.4	6.9	6.3	2.1
F. apii var. *pallidum*								
Isolate 3	112 hrs.	.....	3.8	4.4	5.1	5.1	4.7	
" 45	112 "	.....	2.7	4.2	4.3	4.3	3.0	
" 3	136 "	3.4	4.2	5.1	5.6	5.6	4.8	2.5

The maximum radial enlargement of the thalli of *F. apii* in each of the two tests occurred at 28° C. In the 112 hour series the mean diameter of the thalli of isolate 7 was as great at 30° C. as at 28° C. It is evident that the optimum temperature for vegetative development of *F. apii* is close to 28° C. Some isolates of this pathogen grow as well at 29 to 30° C. as at 28° C. so that the true optimum is probably between 28 and 29° C. (Pl. X: 1).

The isolates of *F. apii* var. *pallidum* made the most rapid growth at 26 and 28° C. (Pl. X: 2). In these tests the results were remarkably uniform for the average diameter of the two thalli of each isolate was identical at 26 and at 28° C. It will be noted that there was a sharp decrease in growth at 30° C. and that isolate 45 in the 112-hour series and isolate 3 in the 136-hour test made a better growth at 24° C. than at 30° C. It is apparent from these results that *F. apii* var. *pallidum* has a slightly lower optimum temperature than *F. apii*. This fungus grows best at 26 to 28° C. and its optimum lies between these two points. The extreme limits of growth have not been determined but the minimum temperature for vegetative growth is slightly below 8° C. and the maximum is above 32° C.

INFLUENCE OF SOIL MOISTURE AND SOIL TEMPERATURE ON THE GROWTH OF CELERY

Celery makes the most rapid growth during the cooler portions of the growing season and when the soil moisture is maintained at a high level. At that time Fusarium yellows is not active and it is only during midsummer when the plant reacts unfavorably to high temperatures and low soil moisture that the disease attains great importance. To aid in an analysis of the relation of temperature and moisture to the Fusarium yellows disease, some knowledge of the influence of these factors on the celery plant is desirable. For this purpose, plants were grown under controlled conditions in the soil tanks.

The soil tanks used in these experiments were similar to the Wisconsin model and the temperature fluctuations were not in excess of ± 0.5° C. Composted soil, high in organic matter, was used. The moisture equivalent of this soil was approximately 40 which is much lower than that of muck soils. In the tests, an attempt was made to determine the approximate minimum and optimum degree of soil saturation for the growth of celery.

The soil was sterilized by steaming for two hours and divided into two portions. One portion was air-dried until the moisture content was 40 per cent of the water-holding capacity. Sufficient water was added to the second portion to adjust the moisture to 65 per cent of the water-holding capacity. A weighed quantity of the soil was dispensed into soil cans of equal size and weight, and five Golden Self-Blanching celery plants of the same aggregate weight were immediately set in these cans. The plants had previously been grown in sterilized, composted soil similar to that dispensed into the cans. All soil was washed from the roots just before the plants were set in the cans. The cans were held in a cool place for 72 hours and then placed in the tanks at the following temperatures: 18, 21, 24, 27, and 30° C. The plants were grown in the tanks from March 7 to May 4, during which time the air temperature varied between 15 and 20° C., and on sunny days in April sometimes reached a maximum of 25° C. or higher.

All plants in the 40-per cent moisture-holding capacity series grew poorly at all temperatures. At the higher temperatures some died within a few days, and only at 18 and 21° C. did all of them survive. It was plainly evident from their appearance that there was insufficient moisture in the soil to support a normal development. An examination at the termination of the experiment showed that only at the two lower temperatures had there been any new roots formed and comparatively few on those plants. Very little new top growth was produced, and the plants were but little larger than at the beginning of the experiment.

All plants in each can of the 65-per cent series survived until the end of the experiment, but those at 30° C. grew slowly and increased only slightly in size (Pl. XIII: 1). The plants grew most rapidly at 18° C. and produced an abundance of fibrous roots. Root development was progressively poorer as the temperature increased above 21° C., but the differences in top growth were not so apparent although the plants were more spindly at 27° C. than at the lower temperatures. Root and top development was superior at 18° C. and the higher content of soil moisture was decidedly productive of a more nearly normal development.

The experiment was repeated with soil moisture adjusted to 50 and to 75 per cent of the water-holding capacity of the soil, and the soil temperatures were held at 20, 22, 24, 26, 28, and 30° C. In this 48-day test, the plants in the lower moisture series grew better than those in the 40-per cent series of the previous experiment, but their development was again decidedly inferior to those in the soil containing more water. The best development again occurred at the lowest temperature, 20° C., but at 22 and 24° C. both root and top growth was only slightly less vigorous than at 20° C. At temperatures above 24° C. development was progressively poorer, and at 30° C. the plants were stunted and somewhat chlorotic. In all cans of the 75-per cent saturation series, the plants grew better than those in the 65-per cent series of the previous experiment, which indicated that the higher moisture content of the soil was beneficial. In these tests the conditions which favored the best development of celery were a comparatively cool soil with a moisture content maintained at 60-75 per cent of the water-holding capacity.

EFFECTS OF SOIL TEMPERATURE AND SOIL MOISTURE ON THE DISEASE

In the original infection tests made in 1917, it was found that Fusarium yellows developed most rapidly when the plants were grown in infested soil at a temperature of approximately 28° C. In later tests reported here the results have been similar and confirm those of the earlier experiments. In conjunction with the soil temperature experiments, the influence of soil moisture has been determined in a series of tests which have also yielded similar uniform results. A description of typical experiments will present an epitome of the entire series and will suffice to illustrate the important role of these environmental factors in the development of Fusarium yellows.

Composted soil, previously sterilized in flowing steam and then infested with pure cultures of the celery pathogens, was used in each experiment. An equal amount of the oat inoculum was added to weighed quantities of sterilized soil so that the plants in each can would be exposed to infection under conditions of uniform soil infestation.

In transplanting celery plants into the soil cans two methods were followed. In one, all soil was washed from the roots and four or five plants of the same size and weight were set in each can. In the other, the small ball of sterilized soil in which the plant had grown for two or three weeks was not removed. The latter method is better since the plants grow uninterruptedly, and the initial symptoms usually appear earlier than in plants with the soil removed.

Numerous isolates of *F. apii* and *F. apii* var. *pallidum* have been used in the temperature experiments, and the variations noted by other investigators in similar diseases caused by other Fusaria have been observed. With the various strains the latent period of infection and the degree of virulence have been the most variable characters. Recently isolated strains were usually more virulent than those carried in culture for several years, but the original isolate of *F. apii* (No. 1) was still virulent after 16 years in culture. Air temperature is another factor which influences the latent period of infection, and the development of yellows was much more rapid when it was above 25° C.

The results of a representative experiment to determine the influence of soil temperatures upon the development of yellows are given in Table 12. In this test two strains of *F. apii* and one of *F. apii* var. *pallidum* were used. The moisture content of the soil was not held at a constant level throughout the experiment, but conditions were favorable for rapid growth at all times. Five plants of Golden Self-Blanching were set in each of two cans at five different temperatures, and the checks included 10 plants in sterilized soil in each tank. A total of 40 plants was grown at each temperature, 30 in infested soil and 10 in non-infested soil. Notes on symptoms were taken 12, 15, 18, and 22 days after the experiment was started, and after 34 days the experiment was terminated. The living plants were removed from the cans and the primary and secondary roots sectioned and examined for evidence of vascular invasion.

The initial symptoms of yellows appeared first in the plants grown at a soil temperature of 28° C. These symptoms were evident after 12 days in plants grown in soil infested with *F. apii*, isolate 1, and after 15 days in

TABLE 12. *Influence of soil temperature on the development of yellows in Golden Self-Blanching celery grown in soils infested with pure cultures of F. apii or F. apii var. pallidum. (Control plants at all temperatures remained healthy.)*

Pathogen	Temperature, °C.	Condition of Plants after														
		12 days			15 days			18 days			22 days			34 days		
		*D.	T. Dis.	H.	D.	T. Dis.	H.	D.	T. Dis.	H.	D.	T. Dis.	H.	D.	T. Dis.	H.
F. apii																
Isolate 1	22	0	0	10	0	2	8	0	5	5	0	8	2	0	10	0
" 42		0	0	10	0	0	10	0	5	5	0	5	5	0	6	4
" 1	24	0	0	10	0	4	6	0	5	5	0	8	2	1	9	0
" 42		0	0	10	0	0	10	0	3	7	0	4	6	1	3	6
" 1	26	0	0	10	0	4	6	0	10	0	0	10	0	0	10	0
" 42		0	0	10	0	4	6	0	5	5	0	5	5	2	4	4
" 1	28	0	5	5	0	8	2	0	10	0	0	10	0	2	8	0
" 42		0	0	10	0	6	4	0	8	2	1	9	0	2	8	0
" 1	30	0	0	10	0	0	10	0	10	0	0	10	0	0	10	0
" 42		0	0	10	0	6	4	0	9	1	1	8	1	1	8	1
F. apii var. *pallidum*																
Isolate 2	22	0	0	10	0	0	10	0	0	10	0	1	9	0	6	4
" 2	24	0	0	10	0	0	10	0	2	8	0	2	8	0	6	4
" 2	26	0	0	10	0	0	10	0	1	9	0	2	8	0	5	5
" 2	28	0	0	10	0	0	10	0	3	7	0	4	6	0	8	2
" 2	30	0	0	10	0	2	8	0	7	3	0	7	3	0	9	1

*D.—Plants dead.
T. Dis.—Plants typically diseased.
H.—Plants healthy

the soil infested with isolate 42. Initial symptoms in the plants grown in the soil infested with *F. apii* var. *pallidum* appeared first at 30° C., but the development of form II of yellows was also more rapid and extensive in those grown at 28° C., even though the primary symptoms appeared a little later at this temperature. The tabulated results show also, that each isolate of *F. apii* was slightly more virulent than the single isolate of *F. apii* var. *pallidum*. The reverse has sometimes been true in other tests, and there is little evidence to indicate that one pathogen is more virulent than the other, although considerable variation has been observed within the group of isolates of both *F. apii* and *F. apii* var. *pallidum*.

Yellows developed slower at both 26 and 30° C. than at 28° C., and the virulence of the isolates, as determined by the number of plants killed, was greater at the intermediate temperature. The total number of infected plants was as great at 30 as at 28° C., but the symptoms were more advanced in those grown at the lower temperature. Yellows developed in 22 of the 30 plants grown at 22° C., but the symptoms were only mildly expressed in most of these after 34 days, and this was true in general of the 20 plants which became infected at 24° C. At this temperature, however, one plant infected with isolate No. 1 of *F. apii* was killed by the disease. The optimum temperature for the development of yellows was approximately 28° C., but the range of temperatures was not great enough in this test to delimit the minimum and maximum for infection.

The results of additional experiments on the influence of both soil moisture and soil temperature are summarized in Table 13, which combines the

PLATE XIII. EFFECTS OF TEMPERATURE AND MOISTURE ON GROWTH OF CELERY AND DEVELOPMENT OF FUSARIUM YELLOWS.

1. Golden Self-Blanching celery grown 55 days in steamed soil at 18 to 30° C. Soil moisture, 65 per cent of water-holding capacity. Best growth at 18° C.
2. Golden Self Blanching celery grown 55 days in steamed soil infested with *F. apii*, isolate 7, temperatures 18 to 33° C., soil moisture at 40 per cent of water-holding capacity. Stunted growth due mostly to low soil moisture. At 33° C. the plants died from the effects of the high soil temperature.
3. Same as 2 with soil moisture maintained at 65 per cent of water-holding capacity. Yellows developed most rapidly at 27 and 30° C. At 33° C. the plants were killed in two weeks by the high soil temperature.
4. Soil infested with *F. apii* var. *pallidum*, isolate 3, moisture at 65 per cent water-holding capacity. Maximum development of yellows at 27 to 30° C.
5-6. Celery grown for 48 days in steamed soil infested with *F. apii*, isolate 87, with soil moisture maintained at 50 per cent of water-holding capacity (5) and 75 per cent of water-holding capacity (6). Soil temperatures 20 to 30° C. The plants grew poorly in the low moisture soil and displayed but feeble symptoms of yellows in comparison with those that developed in the plants grown under more favorable conditions. Yellows developed most actively at 26 to 30° C.
7. Soil infested with *F. apii* var. *pallidum*, isolate 3, soil moisture 75 per cent of water-holding capacity. Yellows most active at 28° C.

PLATE XIV

1. General view of the experimental plats at Kalamazoo in 1914.

2. The formaldehyde plats. (A) 1-50, (B) 1-25, (C) 1-100 applied at rate of 1 gallon per square foot. The poor stand is due to chemical injury.

3. A steamed plat in which yellows was controlled except at the extreme edge where the steam pan did not cover the soil. Note freedom from weeds.

4. A steamed plat in which the steam did not penetrate so deeply as in (3). However, only one diseased plant appeared in this plat during the season.

5. A plat in which mercuric chloride 1-1000 was applied, 1 gallon to each square foot of surface. Fifty-one diseased and 14 healthy plants on August 19. (B) Steamed plat in which potato tubers were not softened at 6 inches. Note that yellows is appearing in this planting.

6. (A) The soil in this plat was treated with 2 per cent $CuSO_4$, one gallon per square foot. Yellows was only partially controlled. (B) The roots of the plants were dipped in lime-sulphur 1-30. The stunted and yellowed condition of the plants shows the ineffectiveness of this treatment in controlling yellows.

7. An untreated plat. All of the plants are infected and the soil is overrun with weeds. Compare with (3), a steamed plat.

8. A portion of the field steamed in 1915. Photographed September 16. The plants are disease-free and have made a vigorous growth. No weeding was necessary in this field during the entire season.

readings of two tests in which the soil moisture was adjusted to four different water-holding capacities and the temperature range was from 18 to 33° C. Control plants were grown in sterilized soil at all the temperatures indicated except at 33° C., where the smaller capacity of the tank made it impossible to grow them in this series. As will be seen later, celery is killed at this soil temperature, and these checks were not necessary.

At 18° C. no symptoms of yellows appeared in any of the plants, and this reading appears to be close to the minimum temperature for infection. The development of the disease was slight at 21° C., and no chlorosis was evident in the leaves at the end of eight weeks, but discolored vascular tissue was present in the secondary roots as evidence of infection. At 24° C. all plants became diseased in the soil infested with *F. apii* and in which the soil moisture was maintained at 65 per cent of the water-holding capacity (Pl. XIII: 3). In the 50-per cent moisture series, at this same temperature, the development of yellows was less evident. The optimum temperatures for the yellows disease in these tests was between 26 and 30° C., with the higher soil moisture favoring a more rapid development (Pl. XIII: 3, 4). The maximum virulence of *F. apii* was manifested at 27 to 30° C., but *F. apii* var. *pallidum* was slightly more virulent at 24 to 27° C. These results check with those obtained in the temperature studies summarized in Table 13. Root development at the lower moisture content was so slight that the plants increased but little in size. Especially was this true of those grown at temperatures from 24 to 30° C. At 33° C. all of the plants died within two weeks without showing any symptoms of yellows (Pl. XIII: 2, 4). This temperature seems to be slightly above the maximum for celery.

In the preceding experiment no disease appeared in the seedlings grown at 18° C. with the soil moisture maintained at 40 and 65 per cent, respectively, of the water-holding capacity, and at 33° C. the seedlings died before they developed any symptoms of yellows. In the next series the temperature range was adjusted in 2-degree steps from 20 to 30° C., and the soil moistures were maintained at 50 and 75 per cent of the water-holding capacity, respectively. Golden Self-Blanching plants were used instead of Golden Phenomenal.

The most favorable temperatures for the development of yellows in this series were from 26 to 30° C. (Pl. XIII: 5, 6). In plants infected with *F. apii*, the disease progressed more rapidly at 28 to 30° C., while those infected with *F. apii* var. *pallidum* showed the most injurious effects at 26 to 28° C. At lower and higher soil temperatures symptoms developed more slowly, and the general progress of the disease was less rapid. Soil moisture maintained at 50 per cent of the water-holding capacity was slightly less favorable for yellows than at 75 per cent. As in the previous series, low soil moisture was less conducive to the development of yellows than a degree of saturation which permitted normal root development. Apparently there is a minimum moisture content of the soil below which infection does not occur because of an unfavorable effect on the celery plant.

Observations have shown that dry soil apparently is not favorable for the development of yellows. The experiments on the relation of soil moisture and soil temperature may provide an explanation for those observations. The moisture equivalent of the celery soils at Kalamazoo is high, and one gram of dried muck will absorb about 1.4 to 1.6 grams of water. When

TABLE 13. *Relation of soil temperature and soil moisture to the development of yellows in Golden Phenomenal and Golden Self-Blanching celery grown for seven or eight weeks in steamed soil infested with pure cultures of F. apii or F. apii var. pallidum. (Control plants at all temperatures remained healthy.)*

Pathogen	Temperature, °C.	Soil Moisture at 40 Per cent Water-holding Capacity				Soil Moisture at 65 Per cent Water-holding Capacity			
		Condition of Golden Phenomenal plants after eight weeks							
		*W.	C.	V.D.	H.	W.	C.	V.D.	H.
F. apii Isolate No. 7	18	0	0	0	5	0	0	0	5
	21	0	0	1	4	0	0	3	2
	24	0	0	3	2	1	1	4	0
	27	2	3	3	0	4	1	1	0
	30	3	2	2	0	2	3	3	0
	33	5	0	0	0	5	0	0	0
F. apii var. *pallidum* Isolate No. 3	18	0	0	0	5	0	0	0	5
	21	0	0	1	4	0	0	0	5
	24	0	1	1	4	0	3	3	2
	27	0	4	4	1	0	5	5	0
	30	0	1	1	4	0	4	4	1
	33	5	0	0	0	5	0	0	0

Pathogen	Temperature, °C.	Soil Moisture at 50 Per cent Water-holding Capacity				Soil Moisture at 75 Per cent Water-holding Capacity			
		Condition of Golden Self-Blanching plants after seven weeks							
		*W.	C.	V.D.	H.	W.	C.	V.D.	H.
F. apii Isolate No. 87	20	0	0	0	4	0	0	0	4
	22	0	0	2	2	0	0	1	3
	24	0	2	2	2	0	4	4	0
	26	1	3	3	0	1	3	3	0
	28	3	1	1	0	2	2	2	0
	30	2	2	2	0	2	1	1	1
F. apii var. *pallidum* Isolate No. 3	20	0	0	0	4	0	0	0	4
	22	0	1	1	3	0	0	2	2
	24	0	2	3	1	0	2	2	2
	26	0	3	3	1	1	3	3	0
	28	0	0	3	1	3	1	1	0
	30	1	0	0	3	2	2	2	0

* W.—Plants wilted or dead.
C.—Plants chlorotic.
V.D.—Plants showed vascular discoloration.
H.—Plants healthy.

such soil contains water equivalent to only 70 per cent of the water-holding capacity, it is barely moist enough to "ball" in the hands. In summer when the moisture content falls below 50 per cent of the water-holding capacity, the temperature may rise considerably because of the low specific heat of the comparatively dry soil and its high caloric absorption. The growth of celery is then checked. On the other hand, if these soils contain enough

water to maintain a rapid growth of celery they do not become hot enough to check the growth of the plant, and optimum temperatures for the development of yellows seldom occur. Thus in seasons of abundant rainfall the disease is much less important than in years when soil moisture is deficient.

Temperature has a dual role as a determining factor in the development of yellows. In the spring the growth of the celery plant is accelerated by comparatively low soil temperatures and a high moisture content, but the pathogen is inhibited by the low temperature. In July and August, under drouth or semi-drouth conditions, soil temperatures approach the optimum for the development of the pathogen. As a result, growth of the plant is checked, and at 28° C. the peak of its susceptibility to yellows is reached. Whether the optimum temperature for the disease is more influential in its effect upon the pathogen or by its inhibitory influence on the growth of celery cannot be decided from these experiments. Since it has been shown that resistance to yellows in some varieties of cabbage breaks down at temperatures somewhat above the optimum for the development of the disease (55), it seems probable that the influence of temperature on the plant is probably as important as the effect on the pathogen.

CONTROL OF FUSARIUM YELLOWS

BY EXCLUSION

The celery industry in Michigan is expanding, and new areas are constantly being exploited for the production of this crop. In most of these sections celery has not previously been grown. In several localities where the acreage is increasing, Fusarium yellows has not yet become a serious menace to the culture of susceptible varieties, and they may yet be grown successfully. In some sections, certain very susceptible varieties are grown for special markets. The history of yellows illustrates how quickly this favorable position with respect to the production of the most profitable varieties may be lost by the introduction of the disease.

The most effective method of protecting those yellows-free areas is by the complete exclusion of celery plants that have been grown in other sections. Successful exclusion of the yellows pathogens may have been accomplished in Florida by using only locally grown plants. No authentic record of the occurrence of the disease in that state has been made. It is true that soil temperatures are unfavorable for the development of yellows during a major portion of the growing season, but it is unlikely that temperature is the only factor responsible for the freedom from infestation in that important section.

The Fusarium yellows disease has recently appeared in serious proportions in the important delta region of California. It was first observed there in 1935 but has been present in southern California for at least 10 to 15 years. The introduction of the disease into the San Joaquin Valley can probably be attributed to the importation of plants from southern California. The dissemination of Fusarium yellows in Michigan by infected plants may be taken as an example of how the shipment of plants, or other materials har-

boring the causal fungi, from farm to farm or district to district, brings about infestation of wide areas. Much of this dissemination could have been avoided by proper regulatory measures to prohibit the shipment of plants from infested areas.

BY ERADICATION

When yellows was first called to the attention of the station pathologist in 1913 the area of infestation was relatively small. Only a comparatively small number of fields were completely infested, but the disease was apparently spreading rapidly. In some fields the infested portions were but a few yards in diameter. At that time it seemed possible that the disease might profitably be eradicated from fields if some treatment could be found which would destroy the causal agent and thus save the land for production of celery. The high valuation of the land and the necessity of obtaining the largest possible income in order to make it profitable for agricultural purposes, limited use of the land to intensive culture of summer celery. This justified the testing of all measures which might be of value in the fight against any further spread. After surveying the infested area in 1913, it was decided to test the value of various treatments in freeing the soil of the causal agent.

Field Experiments of 1914[13]

The preliminary experiments to test the efficiency of various chemical treatments and of steaming the soil were conducted during the summer of 1914. A field was obtained in the south marsh of Kalamazoo on which previous plantings had been ruined by yellows. This field had been abandoned by the grower, and at the time the work was begun practically all of the celery plants on it were dead. A section was chosen which was suitable for the experimental work because of the uniform and general infestation and also because of its location with respect to water and convenience in handling the equipment.

The experimental area was laid out to include 56 plats, each 7 by 7 feet (Pl. XIV: 1). The boundaries of the individual plats were formed by 10-inch boards and these were sunk 6 inches into the muck. Each plat, unless otherwise indicated, was spaded and raked before the treatments were applied and subsequently all necessary precautions were taken to prevent contamination of the treated plats with soil or material from other parts of the field. Standard disinfecting solutions of corrosive sublimate and formaldehyde were used for treating tools used on the plats, and where necessary, the hands of the workers were washed in a 1-1,000 solution of corrosive sublimate when transplanting or weeding operations injected any element of a chance contamination of the treated plats.

The treatment of the individual plats is shown in the diagram of the experimental area. The liquid treatments were applied as "drenches" at the rate of one gallon to each square foot of soil unless otherwise indicated. The solutions were made in 50-gallon vinegar barrels and then siphoned onto the plats and allowed to seep slowly into the soil. Some treatments consisted of applying the solution directly to the row with sprinkling cans just before the plants were set. The rates of application varied and the amounts applied per linear foot of row are shown in the diagram.

[13]M. W. Gardner was associated in the conduct of field experiments in 1914.

DIAGRAM OF EXPERIMENTAL PLOTS AND OF TREATMENTS FOR THE CONTROL OF CELERY YELLOWS, KALAMAZOO, 1914. EACH PLOT 7′ x 7′.

1 Check. Close spacing of plants.	2 Check.	3 Steamed with pan. Potatoes cooked at 12″.	4 Steamed with pan. Potatoes cooked at 12″.
8 Soil drench, $HgCl_2$ 1-1,000.	7 Steamed with pan. Potatoes cooked at 4″ but not at 6″.	6 Steamed with pan over rack. Potatoes cooked at 18″.	5 Deeply spaded and then steamed with rack 6″ below surface.
9 Soil drench, formaldehyde 1-50.	10 Steamed with rack. Potatoes partly cooked at 6″.	11 Air-slaked lime, 1 lb. to 7 sq. ft.	12 Soil drench, 3 oz. $CuCO_3$; 1 pt. NH_4OH; 50 gals. H_2O.
16 Soil drench, formaldehyde 1-25.	15 Soil drench, H_2SO_4; 1-400.	14 Check.	13 Soil drench, 1½ oz. $CuCO_3$; ½ pt. NH_4OH; 50 gals. H_2O.
17 Soil drench, formaldehyde 1-100.	18 $HgCl_2$ 1-2,000, 1 gal. to 2 lineal ft. row.	19 Soil drench, Bordeaux mixture 4-4-50.	20 Deeply spaded.
24 Roots rolled in sulphur.	23 Row drench, $HgCl_2$ 1-2,000, 1 gal. to 2 lineal ft.	22 Roots dipped in 4-4-50 Bordeaux; row drenched with 2½ gals. to 7 lineal ft.	21 Roots dipped in Bordeaux mixture 4-4-50.

WALK — WALK — WALK

SERVICE

WALK

25 Soil drench, H_2SO_4 1-400 + 2 lbs. lime.	26 Soil drench, H_2SO_4 1-200.	27 Roots dipped in lime-sulphur 1-30.	28 Soil drench, $CuSO_4$ 1-50.
32 Soil drench, H_2SO_4 1-200 + 5 lbs. lime.	31 Soil drench, H_2SO_4 1-100.	30 Roots dipped in $HgCl_2$ 1-2,000.	29 Soil drench, $CuSO_4$ 1-200.
33 Soil drench, H_2SO_4 1-100 + 10 lbs. lime.	34 Check.	35 Check.	36 Soil drench, $CuSO_4$ 1-100.
40 Deeply spaded.	39 Soil drench, H_2SO_4 1-400 + 7 lbs. lime.	38 Roots dipped in $HgCl_2$ 1-1,000.	37 Check.
41 Resurfaced with 6″ of subsurface muck.	42 Soil drench, H_2SO_4 1-400.	43 3/8 oz. $ZnCl_2$ per sq. ft. raked into soil.	44 Soil drench, $ZnCl_2$ 1-100.
48 1½ lbs. powdered $CuSO_4$ raked into soil.	47 Formaldehyde 1-100. Row drench, 3 gals. to 7 lineal ft.	46 Soil drench, $FeSO_4$ 1-5.	45 Soil drench, lime-sulphur, 1-30.
49 6 lbs. powdered $CuSO_4$ raked into soil.	50 Check.	51 Formaldehyde 1-240. Row drench, 3 gals. to 7 lineal ft.	52 Plants dipped in "Zenoleum" 1-100.
56 Resurfaced with 6″ of subsurface muck. 3 gals. formaldehyde 1-50 to 7 lineal ft.	55 10 lbs. sulphur raked into soil.	54 Plants dipped in formaldehyde 1-240.	53 Soil spaded at 2 to 3 day intervals and allowed to dry.

SERVICE — WALK

TABLE 14. *Plat records of experiments on the control of Fusarium yellows, Kalamazoo, 1914.*

Plat No.	Treated	Planted	Plants Alive Aug. 12	Diseased and Dead Aug. 19	Apparently Disease-free Aug. 19	Diseased and Dead Sept. 16	Apparently Disease-free Sept. 16
1		July 18	110	53	57		
2		" "	66	58	8		
3	July 18	" 20	65	1	64	2	63
4	" "	" "	64	0	64	1	63
5	" 17	" 18	68	5	63	7	61
6	" 18	" 20	64	0	64	0	64
7	" 17	" 18	67	0	67	5	62
8	" 15	" "	65	51	14		
9	" "	" "	10	5	5		
10	" 17	" "	56	15	41	16	40
11	" 14	" "	65	30	35		
12	" "	" "	67	48	19		
13	" "	" "	67	55	12		
14		" "	66	58	8		
15	July 16	" "	64	55	9		
16	" 13	" "	0				
17	" 14	" "	67	14	53		
18	" 18	" "	59	11	48		
19	" 16	" "	67	54	13		
20	" 15	" "	62	43	19		
21	" 18	" "	64	49	15		
22	" "	" "	62	53	9		
23		" "	60	52	8		
24	July 18	" "	67	45	22		
25	" "	" "	61	47	14		
26	" 16	" 17	60	48	12		
27	" 18	" 18	62	39	23		
28	" 15	" "	55	11	44		
29	" 14	" "	62	21	41		
30	" 18	" "	60	51	9		
31	" 15	" "	67	62	5		
32	" "	" "	67	59	8		
33	" "	" "	66	61	5		
34		" "	60	50	10		
35		" "	66	48	18		
36	July 14	" "	60	27	33		
37	" "	" "	61	37	24		
38	" 17	" 17	61	42	19		
39	" 15	" "	62	51	11		
40	" 13	" "	61	32	29		
41	" "	" "	61	36	25		
42	" 16	" "	60	47	13		
43	" 14	" "	64	45	19		
44	" "	" 18	63	37	26		
45	" 15	" "	58	36	22		
46	" "	" 17	64	57	7		
47	" 17	" "	0	All dead July 28			
48	" 13	" "	61	52	9		
49	" 14	" "	63	59	4		
50		" "	60	50	10		
51	July 17	" "	19	7	12		
52	" 18	" 18	65	51	14		
53	" 15	" "	52	31	20		
54	" 17	" 17	55	41	14		
55	" "	" "	56	50	6		
56	" "	" "	0	All dead July 20			

A steam pan and a steam rack were used in cooking the soil in those plats where an attempt was made to sterilize the infested area with heat. The steam pan was approximately 5 by 7 feet and the rack consisted of four parallel rows of perforated pipes, 5 feet long and spaced 12 inches. In some plats the steam pan was used alone, and in others the rack was sunk several inches into the soil and the pan placed over it. Steam was generated by a stationary, vertical boiler and carried to the pans by a heavy, flexible steam hose. The boiler pressure in the preliminary experiments seldom exceeded 60 pounds, and the soil in the various plats was cooked from 30 minutes to one hour. After steaming each plat, potatoes were

buried in the soil at depths of 3, 6, 12, and 18 inches and left over night. They were examined the following day and the effectiveness of the steaming was judged by the degree of softening. The soil was considered to be satisfactorily sterilized if the potatoes buried at the deeper levels were softened. As will be shown later, the high thermal capacity of the muck soil, which was abundantly supplied with moisture, resulted in a pronounced residual effect of the heat which kept the temperature effectively high for a long time after the steam was shut off. The steam pan and rack used in these experiments did not cover the area within an individual plat. About one linear foot of soil on each side of the pan, in its narrower diameter, was not steamed. The occurrence of diseased plants in the plats where the potatoes were cooked at depths of 12 inches or more can probably be attributed to the re-infestation of the soil by untreated portions from the borders.

Seedling celery plants of the Golden Self-Blanching variety were obtained from a commercial grower in one of the outlying celery districts of Kalamazoo County where yellows had not yet appeared. Except in plat 1, these plants were set 4 inches apart in three rows which were spaced 2 feet. The total number set in each plat varied from 60 to 70. In plat 1 the plants were set 7 inches apart in each direction, according to a system known then as "modern culture". This close planting eliminated the necessity of using boards for blanching.

The plants were set from July 17 to July 20, and thereafter weekly records were made of their condition. In some plats the plants showed evidence in a few days after setting of injury from the chemicals used. The formalin drenches caused severe injury, and at the higher concentrations the seedlings were killed within a few days (Pl. XIV: 2). The number of plants alive August 19, when a complete record was made of the development of yellows, is an indication of the safety of the treatments, for at this time few plants had been killed by the disease. The August 19 record is the last one taken of the condition of the plants in all plats. A later record, made on September 16, included only those plats that were steamed. By August 19 symptoms of yellows had appeared in the majority of the plants in the untreated soil and the records of all the plantings for that date show the comparative value of the various treatments. The subsequent record on the steamed plats was desirable because of the apparent effectiveness, as shown by the August 19 records, of the steaming as a control measure. The condition of the plants in all the plats on August 19 and September 16 is shown in Table 14.

The steamed plats were the only ones in which yellows was satisfactorily controlled (Pl. XIV: 3, 4). In these, the occurrence of a few diseased plants could be accounted for by the failure of the steam pan to cover the entire area. In plat 6 (Pl. XIV: 4), where the steam rack was buried in the soil and then covered with the pan, the heat permeated the entire area. Test tubers were cooked at 18 inches. This demonstrated the effectiveness of steam in controlling yellows when a penetration of the heat to a depth of 12 to 18 inches was attained. No weeds were in this plat, while in the other steamed areas, they grew around the edges where the pan did not cover the soil. The control of weeds, however, was more strikingly demonstrated in the 1915 commercial steaming test.

Despite the large amount of liquids applied to the soil in the drench treatments, none of the chemicals used was of any commercial value in the con-

trol of yellows. The formalin drenches were so toxic that their actual effectiveness could not be determined, but, in plat 51, where 19 plants survived, seven were affected with yellows on August 19. The number of diseased plants in many of the treated plats, however, was fewer than in the controls. While copper sulphate solutions were more effective than the other drenches, in plat 28—where the strongest solution was used—25 per cent of the plants were infected on August 19.

The failure of the fungicidal solutions to control yellows when used at the rate of one gallon per square foot of surface area was probably due to the highly absorptive capacity of the muck soil. The quantity of solution applied was sufficient to saturate the soil and dilution by soil water was probably not sufficient to render the chemicals ineffective. The highly adsorptive capacity of muck soils would probably prevent an effective use of fungicidal solutions in the control of yellows. The effectiveness of steam was thoroughly demonstrated in these preliminary tests and this method was considered of sufficient value to quality to warrant commercial field trials the following season.

Steaming Experiment of 1915[14]

The 1915 experiments were planned to determine the commercial possibilities of steam in controlling yellows and the cost and practicability of treating large areas. In the field chosen for the 1915 test the celery crop had been destroyed by yellows the two previous seasons. Two new steam pans were constructed, one 5 by 7 feet and the other 7 by 7 feet. Each was equipped with a rack and 13-inch nipples, perforted with two 3/16 inch holes about 12 inches below the threads. This permitted the introduction of the steam into the soil 12 inches below the surface. A 21-horsepower vertical boiler generated the steam which was carried to the pans by one-inch, braided, steam hose.

Preliminary records were taken of the soil temperatures at different levels after steaming. The steam was applied at a boiler pressure of 100 to 125 pounds. After vapor escaped freely from the pan the pressure was reduced and the steaming continued for 10 to 15 minutes. The total time used to apply the steam at the combined full and reduced pressure was approximately 20 minutes. Table 15 contains the records made of the soil temperatures at different depths.

The highest recorded temperature was just below the surface because of the pressure generated under the pan. At the 12-inch level, where the steam was released into the soil, the temperature reached 83° C., and four hours later it was 50° C. At a depth of 8 inches the full effect of the steam was not apparent until four hours after the steaming was completed. During this interim the temperature had increased from 60 to 83° C. The steam did not penetrate much below the 12-inch level and 18 inches below the surface, or six inches below the outlet of the nipples, the temperature of the soil was not changed. The comparatively high temperatures recorded at the eight and twelve-inch levels and the slow cooling of the soil was satisfactory evidence that effective sterilization was attained with a 15- to 20-minute application of the steam.

In the experimental field the area chosen for treatment was about 150 by 50 feet. The plat staked out for steaming was approximately rectangular in

[14]Ezra Levin was associated in the conduct of the field experiments at Kalamazoo in 1915.

TABLE 15. *Soil temperatures at different depths and intervals after steaming for 20 minutes with steam pan.*

Depth of Thermometer Bulb in Soil (inches)	Temperature Immediately After Steaming, ° C.	Temperature 4 Hours Later ° C.	Temperature 18 Hours After Steaming, ° C.
2	93	28	22 (same as air temp.)
3	83	65	50
5	43	83	56
8	60	83	
12	83	50	
18	15	15	

outline and was bounded on the south side by a graveled highway, and on the east side by Axel Creek. At the north and west sides were fields of heavily infested soil.

Beginning at the center of the plot, rectangular areas were steamed with two pans in simultaneous operation. The pans were moved after each steaming toward the north and south boundaries of the plats, respectively. In this way a rectangular area the length of the plat was completed before the next one was begun. The workmen were not allowed to cross from steamed to unsteamed soil and when a section was completed, walking on this soil was avoided.

Each section was deeply spaded before the pans were placed in position. A boiler pressure from 125 to 150 pounds was maintained, and all of the sections covered by the pans were steamed as uniformly as possible. Five days were required to complete the steaming of this plat. The work done on the last day was used as a basis for an estimate of the maximum area that could be cooked with two pans in a single day. With two pans and two men handling them, it was estimated that about 3,000 square feet could be treated in one day.

The steaming was completed June 27, and the following day the boundaries of the cooked area were delimited by disinfected, 12-inch, white pine boards. Plants for the plat were obtained from Comstock, Mich., and these were set on June 28. All possible precautions were taken to prevent re-infestation of the steamed soil. For controls, an adequate number of plants of the same variety were set in unsteamed soil. Records of the development of disease were taken at 10-day intervals. The plants were not sprayed in either the steamed or unsteamed section of the field and due to the excessively wet weather Septoria leaf spot developed rapidly in August. This did not interfere seriously, however, with observations on the value of the steaming and its effectiveness in eradicating Fusarium yellows.

Two weeks after the steaming was completed a noticeable difference in the general appearance of the steamed and unsteamed sections could be observed. The unsteamed portion was uniformly covered with a growth of weeds, but these were mostly lacking on the steamed area. A few scattered patches of weeds in the treated soil indicated that the pans had not been set in an overlapping position. In general, about the only noticeable difference between the cooked and uncooked portions in the field was the relative freedom from weeds of the steamed portion.

Three weeks after the plants were set evidence of infection could be detected by the slower rate of growth in the unsteamed section. Records made July 23 of the conditions of the plants in both the steamed and unsteamed areas showed that the stunted condition of those in the untreated plat was due to infection. This was proved by an examination of the vascular tissues of the roots which showed the typical discoloration of Fusarium yellows. No diseased plants were in the steamed section except in isolated spots where the early appearance of weeds indicated that the soil had not been cooked. The plants in the steamed plat grew rapidly because of freedom from disease and because of very favorable moisture and temperature conditions. The relatively low mean temperature of July and August was unfavorable for the maximum development of yellows and consequently no plants were killed by the disease. The stunting of those on the unsteamed areas, however, was evidence of their diseased condition. By mid-September practically all plants in the unsteamed plat were showing effects of either Septoria leaf spot or of Fusarium yellows.

Although the subnormal seasonal temperatures and excessive precipitation during the summer months of 1915 prevented the expression of normal symptoms of yellows in infected plants and somewhat obscured the beneficial effects of steaming the soil, the yellows-free condition of the plants in the steamed soil was evident from their general appearance (Pl. XIV: 8) and in the freedom from vascular symptoms which occurred in the plants in the unsteamed sections. This test of the commercial feasibility of steaming infested soil in the south marsh section showed that steaming was an effective method for destroying the inciting agent in the soil, but that the work had to be done thoroughly and with great care.

Since one purpose of the 1915 test was to determine the cost of steaming infested soil, the records were one of the most valuable features of the experiment. On the basis of this test, it was estimated that the steaming could be done for from $100 to $200 per acre. This total included the cost of the equipment exclusive of the boiler. The losses of individual growers were from two to four times that amount per acre in 1914 and in some subsequent seasons. The flooding of many fields the following year greatly increased the area of infestation and frustrated plans to eradicate or control yellows by steaming the soil.

As an eradicative measure in sections where the disease has only recently been introduced, and where the infested areas are very small and scattered, the use of steam may warrant the cost. A new infestation might be stamped out by a thorough and prompt steaming of the soil. It is doubtful, however, if this method has any practical application in the field control of yellows. The practicability of steaming as an eradicative measure is limited to seed beds.

PALLIATIVE MEASURES

Among the various environmental factors which determine the seasonal incidence of yellows, it has been shown that none is more important than soil temperature. As has been stated elsewhere, the rising incidence of yellows in the Kalamazoo area and its appearance in most of the other celery sections of Michigan can be traced to lowered water tables and to seasons when drouth or excessively high temperatures have prevailed. The most striking example of the influence of moisture supply upon the comparative incidence of yellows is in the north and south marsh celery sections of Kala-

mazoo. Although the soils in those areas are heavily infested with the yellows pathogens, the incidence of disease is much greater in the north section where the water table is lower. In parts of the south marsh the water table is high, and only highly susceptible varieties are attacked by yellows.

The regulation of soil temperatures by sub-surface irrigation is a useful method to utilize in the control of Fusarium yellows. If excessive drainage has not lowered the sub-surface water beyond levels where it can be utilized, soil temperature and soil moisture may be controlled well enough to prevent yellows becoming a serious disease in normal seasons. This can be accomplished on many fields by damming drainage ditches. Normally, for the best development of celery, the water table should be high when the plants are small. In soils where yellows is not serious, the water table should be maintained at 20 to 24 inches when the plants are larger. This will probably give the best results where yellows is not a serious factor in production, but in heavily infested soil it is doubtful if control can be accomplished by maintaining the water level at this depth.

The application of water by means of overhead sprinkling lines has not aided in the control of yellows. In Kalamazoo the usual practice is to run the lines for a few hours several times a week during the hot, dry weather of summer. Usually not more than one-quarter to one-half an inch of water is applied in one day. In dry and hot seasons the muck is seldom wet for more than 3 to 4 inches below the surface. This, of course, merely leads to the formation of shallow roots, which, because of their proximity to the warm surface soil, are more susceptible to invasion by the yellows pathogens.

RESISTANCE TO FUSARIUM YELLOWS

The control of the fusarial wilts of economic plants by the development of resistant or immune varieties has proved to be the most practical and economical method of combating these diseases. Since the pathogens are persistent soil organisms, other methods of control do not provide a permanent solution. The two methods of producing plants resistant to wilt are exemplified in the early work of Orton (32, 33). The technique used by him, and followed subsequently by other investigators in breeding for resistance to fusarial diseases, has been employed in the celery breeding work.

The period of rapid dissemination of Fusarium yellows in Michigan began about 1915, and the problem of control quickly became a very pressing one. The successive failures of plantings in the Kalamazoo section and the alarming spread of the disease to other producing areas necessitated the development of control measures of general applicability. Fortunately, growers had been testing for several years various commercial varieties of celery for adaptability and resistance, and valuable information had been obtained from these trials. The failure of the dwarf strain of Golden Self-Blanching to show any resistance to yellows presaged the disappearance of this variety from the infested sections. The resistant green variety, Newark Market, introduced under the name "Easy Blanching" was rapidly supplanting it. While providing an alternative to the abandonment of these fields, this was a generally unsatisfactory solution of the problem. The forced substitution of green celery for the yellow varieties was a serious handicap to growers. The cultural practices in that section and market demands necessitated the growing of yellow celery. Because of the longer blanching time, the growers were tremendously handicapped in growing and trying to market green celery.

Golden Self-Blanching could be blanched in 10 to 14 days during the summer months, Newark Market, and other similar varieties, required three to four weeks, and this long blanching did not remove all of the green color.

The intensive system of culture in the Kalamazoo section necessitates the use of a variety that matures quickly and one which can be blanched in boards in 7 to 14 days. For the late fall crop blanched in earth or in trenches, slower blanching kinds may be used. Because of the general adaptability of the dwarf strain of Golden Self-Blanching and the universal demand for this variety when breeding work was begun, the first efforts were directed toward the production of a resistant strain which would make possible a general resumption of the culture of yellow celery.

Production of a Resistant Strain of the Golden Self-Blanching Variety

Although some selection work was started as early as 1916, losses of selected plants from soft rot interfered with the breeding work to such an extent that little was accomplished toward producing a resistant strain previous to 1919. At that time the growers were still trying to grow yellow varieties, and various strains of Golden Self-Blanching were included in their plantings. Although these attempts were usually unprofitable they provided material for selection work that otherwise would not have been available.

The season of 1919 was favorable for the development of Fusarium yellows and during the summer a number of fields were observed at Kalamazoo where conditions were satisfactory for selection work. Plantings were observed in which all plants, with the exceptions of the green rogues, were destroyed by the disease. Intermediate types were found, and the heterozygous condition of most strains of Golden Self-Blanching complicated the selection work and made it difficult to locate surviving plants which were representative of the variety. In one field where a trial planting of 12,000 plants of Golden Self-Blanching had been made, only five were alive in September. In general, the surviving plants appeared to be a satisfactory type. With selections from other fields they were brought to East Lansing in October as breeding stock.

Various methods of handling the selected plants to assure successful wintering for seed production were tried. Some of the plants were stored in cold frames protected with a straw covering; some placed in cold storage, while others were potted and held in a cool greenhouse. The two best plants from the group of five which were the sole survivors in one field were among those placed in the greenhouse.

By April 1920, all plants in the cold frames and those in commercial cold storage had been destroyed by soft rot. The greenhouse plants died with the exception of one of the best selections from the group of five previously mentioned. Subsequent observations and experience in handling large numbers of selections, have indicated that plants destroyed by the root or crown type of soft rot during the winter are likely to be individuals that are infected with the yellows pathogens. Some plants may not exhibit any foliage symptoms of yellows and seem to be highly resistant yet the roots often are infected. These plants are usually destroyed by soft rot. The highly resistant plants are seldom attacked by the root form of this disease. If they survive the period when all plants are subject to a destructive soft rot in the

heart leaves, no difficulty is then experienced in bringing them to seed production. This type of soft rot will be considered later.

The surviving plant of the 1919 selections flowered in May 1920, and after careful hand-pollination it produced about one-half ounce of seed which ripened in July. The seed was obtained too late for a field test in 1920, but some of it was sown immediately in heavily infested soil from Kalamazoo and the seedlings were exposed to high temperatures in August and September. The seedlings showed evidence of high resistance (Pl. XV: 1), but the heterozygous nature of the mother plant was evident in the appearance of about 5 per cent susceptible individuals in the progeny. A field test was conducted at Kalamazoo in 1921 and the resistance of the selected strain was compared with commercial Golden Self-Blanching. High temperature and deficient precipitation in 1921 made conditions suitable for the test, and the selected strain showed good resistance in comparison with the commercial sorts (Pl. XV: 3). Because of the dry condition of the soil at the time the plants were set out, the stands of both commercial and resistant strains were unsatisfactory, but the subsequent reaction of the plants indicated that the selected strain was very resistant while the commercial was almost completely susceptible. A duplicate test at East Lansing in cold frames containing infested soil gave similar results (Pl. XV: 2).

The field test supplied evidence of lack of uniformity of the strain as to type. Re-selections were made from the plants grown at East Lansing, and these were held in a cool greenhouse until February when they were exposed to higher temperatures and to strong illumination from 1,000-watt Mazda bulbs. Thirteen plants flowered normally and produced seed in 1922 (Pl. V: 4). The seed again matured too late for a field test, but the resistance of the progenies was determined in the seedling stage by greenhouse tests. As a result of these tests some lines were discarded. Seedling plants of the best ones were planted in infested soil in cold frames and grown until they were large enough to reveal the general type conformation. Four of the most desirable lines were re-selected, and the seed obtained from those selfed individuals was sown in the greenhouse in July 1924, as in the previous trials. Three of the lines proved to be highly resistant, while the fourth was somewhat susceptible.

In cooperation with the United States Department of Agriculture, a plan had been worked out in 1923 for increasing the resistant stocks at the Chula Vista, Calif., field station under the supervision of Dr. I. C. Jagger. Stock seed of the resistant F^2 lines was sent to Dr. Jagger in October 1923, after the completion of greenhouse tests. This early increase of the lines was decided upon for the purpose of obtaining seed for an extensive field test and also to provide an immediate supply for growers whose soils were completely infested with the yellows pathogens.

Reports were given periodically of the progress made in the development of this resistant strain and of the availability of seed for test purposes (12, 9, 13, 26, 27). Seed of the resistant lines was ready to distribute for extensive field trials in 1925. A discussion of the varietal situation at the time of the introduction of the yellows-resistant strain of Golden Self-Blanching is essential to an understanding of the circumstances under which it was first grown in the Kalamazoo section. For several years preceding, and also subsequent to the introduction of this strain, a series of events intervened to check the demand for dwarf strains of Golden Self-Blanching. First of all, the introduction by Vilmorin of the tall strain of Golden Self-Blanching was

quickly followed by a decline in the demand for the old, short strain. Moderately resistant varieties like "Wonderful" had been in use for several years and met the immediate need for a yellow celery to plant in infested soil. The introduction of the "Plume" types at this time marked the beginning of a new era in celery production in Michigan. The successful use of such varieties by a few growers with infested soils quickly led to their general cultivation in the Kalamazoo section. Because of the success which practically all growers had with this celery, they were reluctant to test the new Vilmorin strain. After a few successful trials, however, plantings of this variety increased rapidly. Within a comparatively short time all of the acreage in the Kalamazoo section was planted either to this strain or to Plume types. These new celeries were to dominate the varietal preferences for the next decade.

The introduction and general adoption of Golden Plume and the tall strain of Golden Self-Blanching[15] occurred during the period of breeding for resistance in the short strain of Golden Self-Blanching. Consequently, when the resistant strain was ready for dissemination the growers no longer wanted the old type plant. The quick-blanching kinds became popular with the growers for several reasons. The shorter time required for blanching was a great advantage in the production of an early market celery, and during cool weather, when the short strain of Golden Self-Blanching was difficult to blanch the new types could be prepared for market in a much shorter time.

Because of the changed conditions regarding varieties in the Kalamazoo section, the resistant short strain of Golden Self-Blanching never gained widespread use. Some growers who made trial plantings to compare it with the tall strain and Golden Plume were critical of its blanching qualities. In these instances the comparisons were made with the new varieties and not with the parent type. In plantings made of the resistant strain at Kalamazoo for determining the resistance and the desirability of this strain for commercial purposes, and which were examined by competent horticultural specialists, any variations that were noted were of such minor importance that the strain was pronounced equally as good as commercial stocks of the same variety (Pl. XV: 4, 5).

Production of the Curly Leaf Easy-Blanching Variety

In 1921, a season favorable for yellows, most of the plantings of celery in the areas of heavy infestation at Kalamazoo were of resistant green varieties, mostly Newark Market. The resistance of this variety was sufficient to assure a crop under conditions where the yellow sorts would fail, but in hot and dry seasons the disease frequently affected a large percentage of the plants in some fields. During the summer of 1921, while examining fields of Newark Market in which yellows had developed to some extent, one plant was observed which had an attractive appearance. The leaves were curled and ruffled in an unusual way. The foliage was also lighter in color and seemed to presage an improvement in blanching qualities over the parent strain. This plant was brought to East Lansing and carried through the winter. Seed was obtained in the summer of 1922 and was immediately tested for resistance and type. The seedlings were uniform, and the resistance was superior to that of Newark Market.

[15]The tall strain of Golden Self-Blanching is now generally referred to as "Tall Golden", "Tall French Strain", or "New Golden".

Selected F^1 seedlings were carried through the winter of 1922 and seed was obtained from four of these selections. The F^2 seedlings were uniformly like the parent plant in general appearance and the resistance to yellows, as in the F^2 generation, was superior to that of Newark Market. The stock seed was increased in California and was distributed to growers for the season of 1925 under the name, "Curly Leaf Easy-Blanching". Curly Leaf Easy-Blanching has been tested in the field under various seasonal conditions and has shown high resistance to yellows. As will be shown later, it is much more resistant than most of the green celeries. This variety has a distinctive appearance because of the ruffled foliage, a character which is evident even in the seedling stage. Curly Leaf Easy-Blanching is adapted for use in infested soil where a quick-blanching green celery is needed and especially where the demand is for a variety that will blanch in storage. At one time it had considerable popularity as being the only celery of the green type which would blanch in storage.

Development of Michigan Golden from the Tall Strain of Golden Self-Blanching

The relative unimportance of yellows in Michigan from 1922 to 1928 when practically all growers were able to grow disease-free crops of Golden Plume and the tall strain of Golden Self-Blanching obviated the necessity for other resistant strains. While both of these varieties at the time of their introduction were more resistant than the old dwarf strain, the absence of yellows in plantings of them, especially at Kalamazoo, cannot be attributed solely to inherent resistance. Sporadic outbreaks of the disease were observed in Kalamazoo fields. In all instances these occurred in soils where conditions were most conducive to the development of yellows. Temperature and moisture were less favorable than average during this seven-year period, and those factors, in conjunction with the comparatively greater resistance of Golden Plume and Tall Golden, made it possible to produce crops on fields where an abundant supply of moisture was maintained. The failures occurred where excessive drainage depleted the soil moisture.

From 1922 to 1928 there was no opportunity to make selections in commercial fields of the two varieties commonly planted. The season of 1929 was characterized by drouth and high temperatures in July and August and yellows developed extensively in plantings of Golden Self-Blanching (tall) and also in some strains of Golden Plume. Fields were observed in which the disease was destructive enough to kill most of the susceptible plants. In all fields there were surviving off-type plants but occasional ones had the true type conformation of Golden Self-Blanching. Several selections were made from these fields, and one especially valuable plant was found. Unfortunately all of those were ruined by a heart rot in Michigan of the following year. This rot has proved annoying and has been destructive of breeding stock. Several selections of outstanding merit were attacked and ruined before methods were devised for checking the development of the disease. Since it is so prevalent in plants saved for seed production, a brief description of the disease and methods of control are presented here.

The plants are usually placed in 10-inch pots in the fall and shifted during the winter to 12-inch pots. They are kept growing slowly in a cool house or deep cold frame where the temperature is maintained below 50° F. Usually no trouble is experienced with the plants until the middle of February and later. Just preceding the development of seed stalks and during the

time when the stalks are beginning to emerge, the plants are susceptible to heart rot. The disease usually develops suddenly and the heart of the plant may be ruined within 48 hours unless the decay is checked in the earliest stages.

The first evidence of the disease is a browning of the margins of the leaflets in the heart of the plant, usually those on the emerging seed stalk. If the seed stalk has not started to elongate, the youngest heart leaves are attacked. All young leaves are susceptible, but those on the seed stalks are most commonly affected. The initial symptoms are similar to those of the disease known as "blackheart". Immediately following the killing of the leaf margins, a soft decay begins and advances rapidly through the heart of the plant, which may be destroyed in 48 hours. The decay is a typical bacterial soft rot.

It has not been possible to prevent the development of this trouble in the stock plants by modifying the cultural conditions. Some years the disease seems to develop in the majority of the plants regardless of the method of handling them prior to the period of greatest susceptibility. It is possible to check the disease if the affected plants are treated before the rot has reached an advanced stage. It is necessary to make a daily inspection during February, March, and April when the formation of seed stalks occurs. Immediate excision of the affected portion of the heart, followed by a thorough spraying of the cut surfaces and of the adjacent leaves with a freshly prepared solution of Semesan has proved to be the most effective method of checking this disease. A solution stronger than 0.25 to 0.50 per cent should not be used and the liquid should be sprayed as a fine mist over all portions of the heart, especially on the surfaces exposed by the excision of the diseased tissues. This treatment has saved some of the best selections. A 1931 selection was seriously affected with heart rot in March 1932, and the seed stalk was destroyed. Fortunately a shoot developed later from an adventitious bud and by careful handling during the summer a moderately strong plant was obtained and potted in the fall. The plant was again attacked by heart rot in the spring of 1933, but it was saved by the Semesan treatment and produced a small amount of seed. In this instance seed was obtained in the third year of the plant's growth.

Usually favorable conditions for yellows prevailed during the summer of 1930, and the disease was prevalent in all of the infested areas in Michigan. Many plantings of tall Golden Self-Blanching were entirely destroyed and the previously resistant strains of Golden Plume were seriously affected. Green varieties, usually moderately to highly resistant, were badly diseased at Kalamazoo. The experiences of this season convinced many growers that it was no longer advisable to plant the tall strain on infested soil. The conditions in Kalamazoo County were approaching those of 1916-'18, when the culture of yellow celery was discontinued and it was necessary to use green varieties.

The general incidence of yellows and its destructive effect in some fields made it possible to select very promising plants. In one field of Golden Self-Blanching several surviving plants of a good type were found and those plants were saved for seed production. Selections were also made in other plantings, and those plants were carried through the winter in a cool greenhouse, but in March heart rot destroyed all but one. The surviving plant appeared to be much stronger and less susceptible to the marginal burning of the young leaves. Approximately one-half ounce of seed was obtained from it in July.

PLATE XV

1. Michigan State College yellows-resistant Golden Self-Blanching celery (short) and a commercial strain of the same variety grown in infested soil. The seedlings of the Michigan State College strain are resistant.

2-3. Michigan State College strain compared with commercial Golden Self-Blanching in cold frame test in 1920 (2) and in the field at Kalamazoo in 1921 (3). The comparable resistance of commercial and the yellows-resistant strain is demonstrated in these tests.

4. Commercial Golden Self-Blanching (foreground) and Michigan State College strain of the same variety growing at Kalamazoo in 1929.

5. A single plant of yellows-resistant Golden Self-Blanching celery (short) grown at Kalamazoo, in 1929 in heavily infested soil. This plant shows the generally desirable characteristics of the selected strain.

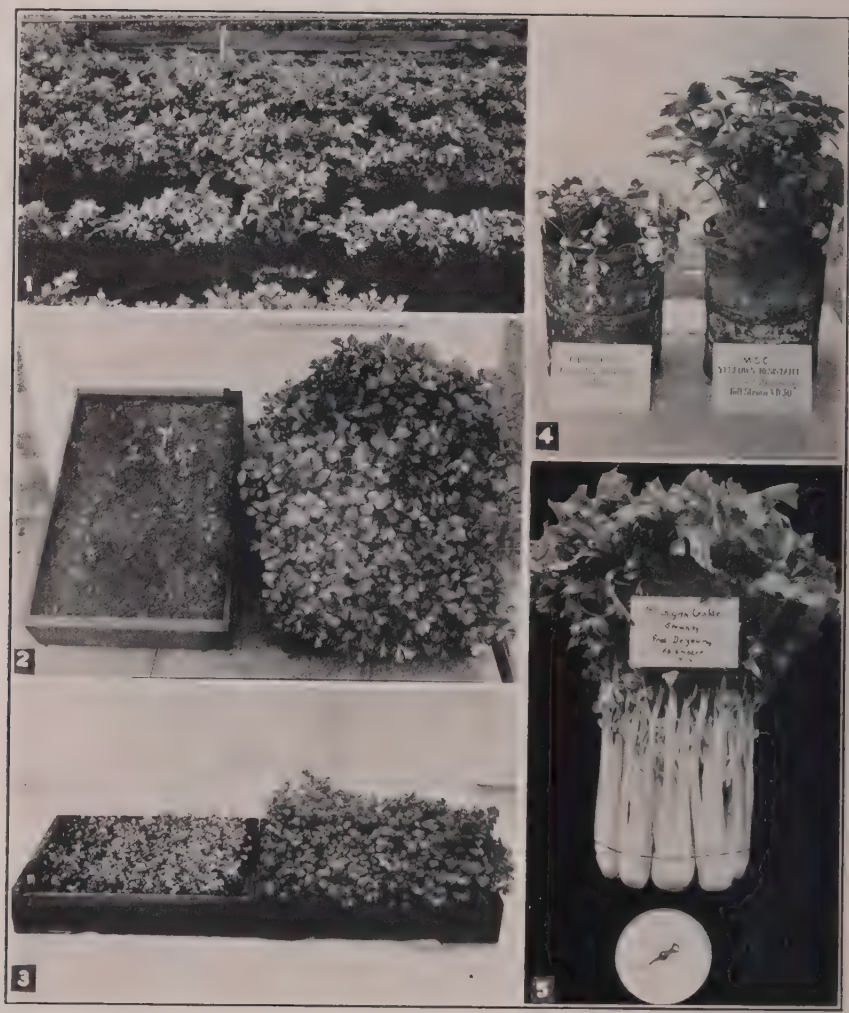

PLATE XVI

1. A resistant celery plant in a planting of tall strain, Golden Self-Blanching at Kalamazoo, July, 1931. Except for resistant green rogues this was the only disease-free plant in this five-acre planting. Both resistant and susceptible seedlings were grown from this plant.

2. The F^1 test for resistance of Michigan Golden. Note the great susceptibility of commercial Golden Self-Blanching (tall) and the apparent immunity of the selected strain. Seed sown in soil infested with many isolates of *F. apii* and *F. apii* var. *pallidum*.

3. The F^2 test for resistance of Michigan Golden. The resistance shown in the F^1 generation has been maintained in later progenies. Commercial Golden Self-Blanching (tall) for comparison.

4. Commercial Golden Self-Blanching and Michigan State College strain V. D. 30 (Michigan Golden) grown in infested soil at 28° C. for 30 days. The resistance of Michigan Golden does not break down at high temperatures.

5. Twelve plants of Michigan Golden taken in consecutive order from the row in a planting at Kalamazoo in 1934. Weight of 12 plants, prepared for market, 16 pounds. In plantings on infested soil Michigan Golden out-yields any of the commercial strains of self-blanching celery.

PLATE XVII

1. Field test of three rows of Michigan Golden at Comstock, Michigan, in 1933, in a five-acre planting of Golden Self-Blanching (tall) ruined by yellows.

2. The same field in 1934 planted with Michigan Golden. Despite extremely favorable conditions for yellows no diseased plants appeared in this planting.

3. Six rows of Michigan Golden (right center) growing beside a three-acre planting of Golden Self-Blanching (tall) at Comstock, Michigan, August, 1933. The commercial strain was destroyed by yellows. No plants of Michigan Golden became infected.

4. Comparison of resistance of Michigan Golden (left) and Early Fortune, one of the most resistant commercial strains of Golden Plume. Note the stunted growth and uneven stand in Early Fortune due to yellows. The plants have been dusted with copper-lime dust.

5-6. Michigan Golden at Kalamazoo, August, 1934. Note height of plants (30 inches) and uniformity in the row. The close planting (4 inches) at Kalamazoo prevents the plants from attaining a larger diameter.

7. Cages in which selected celery plants are grown to prevent cross pollination. These cages are similar to those used by Ferry-Morse Seed Company and to whom the writers are indebted for loan of diagrams.

PLATE XVIII. VARIETAL REACTIONS TO YELLOWS.

1. Two strains of Golden Plume in a planting at Kalamazoo, July, 1931. Golden Phenomenal completely susceptible (right) and Golden Prize, moderately resistant.

2. A planting of "Hoover Special" (center) at Kalamazoo, July, 1931. This variety is a completely susceptible strain of the Plume type and is probably identical with Golden Phenomenal. In planting these varieties Kalamazoo growers lost many thousand dollars in 1931.

3-4. Newark Market, a green variety, at Kalamazoo, 1920. The thin stand and stunted condition of the plants are caused by yellows. The green varieties are moderately resistant but in hot seasons they may be seriously affected by the disease.

5. Two green rogues in a planting of Golden Self-Blanching at Kalamazoo, July, 1931. A resistant strain of Golden Plume in the background. Most strains of self-blanching celery contain mixtures of green kinds which are somewhat resistant to yellows.

6. A planting of Early Fortune at Kalamazoo in July, 1933, showing about half of the plants ruined by yellows. This "Plume" variety produced good crops on infested soil for several years but increasing amounts of disease forced growers with the drier soils to discontinue its culture.

Some of the seed was sown immediately in soil heavily infested with inoculum prepared from the most virulent strains of *F. apii* and *F. apii* var. *pallidum*. Extremely high resistance was manifested at all stages of growth by the F^1 plants and the seedlings were apparently of a uniform type (Pl. XVI: 2). The uniform appearance of the seedlings and the high resistance of all plants to these virulent strains, indicated that this possibly was an immune strain which might maintain this resistance in subsequent generations. In order to be prepared for the 1933 season if further tests of the F^1 and of the F^2 generations proved the high resistance to be stable, it was decided to make a small increase of the stock. The distribution of this seed was contingent upon the results of the F^2 tests which could not be run until seed was obtained from the F^1 selections.

Twenty-two plants were selected from the F^1 seedlings grown in the greenhouse, and these were potted and carried through the winter. The following summer they produced approximately one pound of seed. A composite sample was sown in infested soil, and the seedlings showed the same degree of resistance as the F^1 plants (Pl. XVI: 3, 4). In October the increase from the seed sent to California a year previously was received. The F^2 seedlings from this lot of California-grown seed were just as resistant as the original F^1 plants, and, so far as could be judged from their appearance they were uniform in type. It was apparent from the tests of the two lots of seed, one grown at East Lansing and the other in California, that the F^2 generation was also extremely resistant, if not immune. The first reports on the development of this variety were released after the F^2 tests were completed (28, 29).

Field tests of this new strain were conducted at East Lansing and at Kalamazoo in 1932 with F^1 seedlings and at Kalamazoo in 1933 with plants of the F^2 generation. In addition, practically all of the 60 pounds of seed grown in California was used by Kalamazoo growers for trial in 1933. In those plantings the strain maintained a very high resistance to yellows (Pl. XVII: 1, 2, 3, 4). No disease developed in any field planting, but in some of the greenhouse tests in which the soil was heavily infested with a mixture of strains of strong virulence, an occasional seedling became diseased. Under field conditions the plants appear to be immune and under greenhouse conditions of the most severe kind fewer plants than one in a thousand have shown symptoms of yellows. Under the most severe conditions in Kalamazoo fields in 1933 and 1934, seasons extremely favorable for yellows, Michigan Golden was not only highly resistant but it demonstrated its value as a substitute for the commercial varieties of yellow celery. In comparative tests with Golden Self-Blanching and Golden Plume, the plantings of the former have been completely ruined by yellows, the best strains of Golden Plume have shown from 15 to 40 per cent disease, while Michigan Golden has exhibited no symptoms of yellows and has produced excellent crops.

Michigan Golden appears to be intermediate in type between Golden Self-Blanching and Golden Plume. The stalks are longer than those of most strains of Golden Plume, but the base is like that of the tall strain (Pl. XVII: 5, 6; Pl. XVI: 5). The foliage characters are distinct for the variety, but the leaflets resemble those of Golden Plume more than they do the sharply serrate ones of Golden Self-Blanching.

In other states Michigan Golden has given satisfactory results when tested under conditions favorable for the development of yellows. In Ohio, New

York (52) and Colorado this variety has produced satisfactory crops when grown in soils where commercial varieties have failed. The results of Wilson (57) at Celeryville, Ohio, in 1933 are unusual. In this test he reports that 6.8 per cent of the plants developed symptoms of yellows. Under equally severe conditions during the same season at Kalamazoo no disease developed in any of the numerous field plantings and none in the field test at East Lansing where the soil was heavily infested with many strains of the pathogens. Rykers' tank tests have indicated that Michigan Golden is an immune variety (40). From our tests it seems best to consider it as highly resistant rather than immune. A recent report from Minnesota (1) records the high resistance and generally satisfactory performance of Michigan Golden in that state.

Resistance of Michigan Golden and Other Selections Compared with Commercial Varieties of Yellow and Green Celery when Grown under Conditions of Uniform Soil Infestation

Field tests of the resistance of Michigan Golden and other selections in comparison with commercial varieties of yellow and green celery were conducted at East Lansing in 1933 and 1934. There appears to be considerable variation in certain strains or varieties of celery. Some growers have reported Golden Plume as resistant while others have found it susceptible. Periodic claims are made for the resistance of certain varieties, and there is no unanimity of opinion as to the resistance or susceptibility in some of the varieties or strains most commonly grown in the Kalamazoo area. A great deal of the variability can be explained by the dissimilarity of soil conditions. Some of the celery sections at Kalamazoo are excessively drained and the water table is low. These soils are warmer and yellows develops more quickly and destructively than in fields where the water table is higher. Another cause of variability is the existence of more than one strain of a variety. As will be shown later, there is a great variation in the reaction of different strains of presumably the same variety when grown under uniform conditions. Still another cause of the divergent results reported is variability in the degree of soil infestation with the yellows pathogens.

Seed of the various commercial varieties of celery was bought on the open market, or samples for trial were donated by seedsmen. An attempt was made to obtain seed of the same variety from more than one source. The acquisition of a large number of samples of Golden Plume seemed desirable because of the extreme variability reported in this variety. The seed was sown in a cold frame in sterilized soil, and the seedlings were large enough to set in the field about the first week in June. The seed of many varieties germinated so poorly in both seasons that not enough plants could be obtained for a test. In other varieties the germination was so low that fewer than 50 plants were transplanted to the field. About 150 plants of each variety were used where this many were available. The field soil was a sandy loam which had been heavily manured for several successive years previous to the beginning of this test. It had been heavily infested with inoculum prepared from the most virulent strains of *F. apii* and *F. apii* var. *pallidum*. The fungi were first grown in flasks of sterilized whole oats, and composted manure was then infested with the oats when they were completely overgrown by the mycelium. The manure was then again composted for several weeks, spread uniformly over the field and plowed deeply into the soil. This procedure had been repeated two or three times previous

to the test. The plat was watered by an overhead sprinkling system, and cultural practices, including spraying for control of leaf blights, were comparable with those used in commercial fields.

The seasons of 1933 and 1934 were ideal for yellows, and the disease appeared early in the most susceptible varieties. The readings were taken each year in mid-July after yellows had become serious in Golden Phenomenal and Golden Self-Blanching. Counts were made of the number of plants showing: (a) definite symptoms of yellows; (b) those killed by the disease; (c) those showing no symptoms of infection. It is believed that the records show the comparative resistance and susceptibility of varieties. They do not record their maximum resistance and susceptibility, for many more plants became infected later, and there was an increase in the total number succumbing to the disease. Because of the erratic course of the disease late in the season, when changing temperature and moisture conditions may markedly alter the appearance of diseased plants, the mid-summer records provide a more reliable index of the comparative resistance of the varieties, especially when the seasonal conditions have been very favorable for the development of yellows. It will be observed from the results in Table 16 that by mid-July practically all plants of the highly susceptible varieties were diseased. The percentage of yellows in the other varieties represents their susceptibility when compared with Golden Phenomenal. Using Michigan Golden as the standard, the same rule applies with respect to resistance.

Due to difficulties in obtaining seed of these varieties for the 1933 trials and to the poor germination of some lots which failed to provide plants for the 1934 tests, tests of some varieties were conducted for only one season. In those grown in 1933 and 1934 there were some seasonal variations in the incidence of disease, but these variations were not sufficiently great to alter the general ranking of these varieties in the preceding season. Varieties susceptible in one season did not exhibit a contrary reaction the following year, even though the percentages of disease may have differed considerably.

The higher resistance of the green varieties in comparison with the self-blanching kinds is clearly brought out in the results of the two-year test. These results confirm the field observations of many preceding seasons that native resistance to yellows is greater in the green than in the yellow celeries. Those reactions, however, can not be interpreted as indicating what the varieties may do in commercial plantings under different seasonal or soil conditions. Giant Pascal, for instance, in those tests showed a much lower percentage of disease than occurred in the 1933 field tests at Kalamazoo, when 60 per cent of the plants were infected with yellows. Although only 34 per cent of the plants of Newark Market became diseased in the 1934 test, in the hot, dry seasons from 1919 to 1922, fields were observed at Kalamazoo in which practically all of the plants were affected (Pl. XVIII: 3, 4). Among the green celeries, Michigan State College Curly Leaf was equalled in resistance only by Pride of the Market.

The commercial self-blanching varieties as a group were very susceptible to yellows. Golden Phenomenal, which belongs to the Plume group, was the most susceptible of all yellow celeries. Little less so, was the tall strain of Golden Self-Blanching and Golden Detroit. Some of the commercial strains of "Tall Golden" contain a rather high percentage of resistant green rogues and this, in part, accounts for much of the variation in susceptibility in this test. Pure lines of this variety are extremely susceptible, and when planted in infested soil all plants become diseased if soil temperatures

TABLE 16. *Resistance to Fusarium yellows of Michigan Golden and other selections compared with commercial varieties of green and yellow celery. Field tests at East Lansing, 1933 and 1934.*

Variety	Source	July 18, 1933		July 16, 1934	
		Per cent of Plants			
		Diseased	Dead	Diseased	Dead
GREEN VARIETIES					
Columbia	Abbott & Cobb	25	0	33	8
Meisch Green Spl.	"	29	0		
Winter King	"	8.4	0		
Full Heart Easy-Blanching	"	29	0	10	0
Sweetheart	"	20	0	11	1
Full Heart Easy-Blanching	Alexander Forbes & Co.	3.5	0		
Newark Market	"	12.5	0	34	1
Giant Pascal	Ferry-Morse	14	0	34	12
Utah	"	10	0		
Fordhook	W. Atlee Burpee	7	0		
Bokay	Stump & Walter	26	0		
Covent Garden Red	"	1	0		
New Earligreen	"	0	0	10	5
Salt Lake	Joseph Harris Co.	4	0	32	8
Winter Queen	Vaughn Seed Co.	1	0		
Pride of the Market	Grand Rapids Growers', Inc.	0	0		
Dyer Special	Tether Seed Co.	8	0		
Mont Blanc	Carter's Tested Seeds			22	6
Paragon	F. H. Eberle			3	1
Curly Leaf Easy-Blanching	Michigan State College	0	0	0	0
SELF-BLANCHING VARIETIES					
Golden No. 14	Abbott & Cobb	90	0		
Golden Phenomenal	"	97	0		
Early Fortune	"			8	0
Golden Plume	Alexander Forbes & Co.			25	10
*Golden Prize	"			99	50
Golden Phenomenal	"			100	16
Golden Detroit	Ferry-Morse Co.	100	29	100	4
Florida Golden	"			6	0
Golden Self-Blanching (Tall)	"	64	3	95	3
Golden Plume	"	41	9	41	2
Golden Phenomenal	"	100	6	96	5
Golden Wonder	Hart & Vick	36	0		
Golden Plume	Vaughn Seed Co.	11	0		
Golden Self-Blanching (Tall)	"	97	0		
Golden Self-Blanching (Dwf.)	"	50	0		
White Plume	"	11	0		
Paris Golden	Stump & Walter	6	0		
Paris Select	Grand Rapids Growers', Inc.	50	0		
Golden Prize	Tether Seed Co.			20	1
Golden Self-Blanching (Tall)	"			92	10
Michigan Golden	Michigan State College	0	0	0	0
Golden Phenomenal, 1931 Selection, F_2-1-14	"			14	0
Golden Self-Blanching (Tall) 1931 Selections: F_2-2-11	"			0	0
F_2-3-8	"			11	0
F_2-2-9	"			0	0

*The plants of this variety were like Golden Phenomenal in general appearance and susceptibility. Though labeled "Golden Prize" the seed was not of this variety.

are favorable. Varieties like Paris Golden, which are more resistant than the short strain of Golden Self-Blanching, have apparently obtained this higher resistance from hybridization, in which one of the parents was a variety belonging to the green celeries. This is evident from the general appearance of the plants which are darker in color and blanch much slower than typical varieties of the self-blanching group.

As was anticipated, the various commercial strains of Golden Plume showed different degrees of resistance. There was also considerable varia-

tion in type. Strains which adhered to the true Golden Plume conformation were intermediate in susceptibility between the green celeries and the self-blanching kinds. Some of the newer strains, like Florida Golden, were more resistant than typical strains of Golden Plume. These are apparently of hybrid origin, in which green celeries have contributed resistance and slower blanching qualities. Early Fortune has been grown successfully for a number of years at Kalamazoo, but during the last five years yellows has increased in plantings of this variety, and it can be grown no longer in some of the localities where the water table is low. In this test it ranked next to Florida Golden in resistance, and in general it is one of the best strains of the Plume type. In 1933 at Kalamazoo, 20 to 40 per cent of the plants which were grown for comparison with Michigan Golden were affected (Pl. XVIII: 6). Forbes' strain of Golden Plume showed a higher percentage of yellows than usually develops in commercial plantings. Excessive losses from yellows have forced many growers to discontinue planting this variety.

The high resistance of Michigan Golden in those tests confirmed all previous records of its performance. Three replicate plantings were made in the 1934 plats so that a large number of plants might be available for observation throughout the growing season. No yellows was observed in any plant of this variety. Like all other yellow kinds, it was adversely affected by the unusually high temperatures in June and July. The reaction to these temperatures was expressed as a dwarfing of some plants. This was at first interpreted as evidence of infection, but examination showed that the roots were entirely free of any fungous invasion. The plants recovered after a few days of lower temperatures, and although air temperatures were above normal throughout the entire season and conditions were exceptionally favorable for the development of the yellows disease, no plants were affected.

Of the three selections which were made from plantings of the tall strain of Golden Self-Blanching in 1931, F^2-2-11 and F^2-2-9 were most resistant. Strain F^2-2-11 was superior as the plants were more resistant and conformed closely to the parent type. In the 1935 tests at Kalamazoo this selection did not make as favorable showing as in 1934 and re-selection work is being continued.

It is significant to compare the resistance and susceptibility of varieties grown 20 years ago with those in use today. This is possible through records made at Kalamazoo in 1915 in the experimental work on the control of the Fusarium yellows disease. Seed of most of the commercial varieties grown at that time was sown in steamed soil on the experimental plats in the south marsh section. The seeding was made late in June, and the plants were not set in the field until August. A small number of plants of each variety was transplanted to heavily infested soil, and the observations and records on the reaction to yellows were made October 26. Despite the late date at which those records were taken, the plants had not been injured by frosts. The weather had not been favorable for yellows, rainfall was excessive through the summer and the mean temperature was considerably below normal. The usual foliage effects of the disease were not noticeable and the only conspicuous sign of infection was dwarfing. Plants were pulled at random from each varietal plat, and the amount of dwarfing and degree of vascular discoloration were used as measures of resistance or susceptibility. The reactions of some of the varieties are given in Table 17. A few of them

TABLE 17. *Comparative susceptibility of commercial varieties of celery to Fusarium yellows in 1915. Test at Kalamazoo, August-October.*

Variety	Number Plants Examined	Condition of Plant			
		External Appearance		Internal Appearance	
		Stunted	Normal	Vascular Discoloration	Normal
Golden Self-Blanching (Orig.)	10	10 (markedly)	0	10 (very marked)	0
Golden Self-Blanching (French)	9	7 (slightly)	2	7 (moderate)	2
Golden Self-Blanching (American)	10	10 (moderately)	0	10 (slight)	0
Giant Pascal (French)	10	0	10	6 (slight)	4
Giant Pascal (American)	10	10 (markedly)	0	10 (very marked)	0
Columbia (American)	6	6 (markedly)	0	6 (slight)	
Winter Queen	10	6 (moderately)	4	6 (slight)	4
Winter King	10	10 (markedly)	0	10 (slight)	0
White Plume	14	11 (markedly)	3	11 (very marked)	3
Perfected White Plume	16	12 (moderately)	4	12 (very marked)	4
Pink Plume	10	10 (markedly)	0	10 (slight)	0
French Success	10	10 (markedly)	0	10 (very marked)	0
New Rose	10	9 (slightly)	1	10 (very marked)	0
Boston Market	10	5 (slightly)	5	5 (slight)	
Rose Ribbed Paris	10	7 (slightly)	3	7 (slight)	3
Winter Reliance	13	12 (slightly)	1	12 (very marked)	1
Kalamazoo	10		10	5 (very marked)	5

are still grown in Michigan and other states. The varieties omitted are no longer in the varietal lists.

The reactions of Golden Self-Blanching in the 1915 trial were typical of the variety at that time and showed its great susceptibility to the Fusarium yellows disease. In the 1933 test this same variety appeared to be much less susceptible even though conditions were much more favorable for the disease than in the earlier experiment. The seed source was the same for the two seasons. While this greater resistance in 1933 may have been acquired through breeding in the interim since 1915, there is also the possibility that the prolonged absence of contact with the pathogens may have affected the virulence of the pathogens for that variety. Golden Self-Blanching has not been grown at Kalamazoo since 1920 when its great susceptibility forced the abandonment of its culture. Golden Detroit, a newer selection of Golden Self-Blanching of the dwarf type, was completely susceptible in the 1933 and 1934 trials.

In the 1915 trials the green varieties were moderately susceptible to yellows, most of them exhibiting considerable tolerance. A comparison of susceptibility in 1915, and in 1933 and 1934 of Winter Queen, Winter King, and Giant Pascal shows that these varieties were more resistant in the recent tests. Winter Queen was one of the most resistant commercial green varieties in the 1933 trial, but it was susceptible in 1915. A similar reaction was shown by other green kinds. The green varieties have not been grown in Michigan in the infested districts for about 15 years. While no conclusions can be drawn from these results, because of the limited amount of data for comparison, there is suggested the possibility that prolonged separation of a specific susceptible variety from the yellows pathogens may bring about a reduction, at least temporarily, of the virulence of the pathogen for that variety.

SUMMARY

Celery is one of the most important truck crops grown in the United States, and Michigan usually ranks second or third in acreage with a farm value of $2,500,000 in normal seasons.

Since 1913, when it was first observed, the Fusarium yellows disease has been destructive at Kalamazoo and in other districts of similar intensive production. The disease has been reported from most celery-producing states and in some sections it has caused serious losses.

Two forms of the disease, distinguishable by symptoms produced in self-blanching varieties, occur generally in Michigan celery districts. A description of the symptoms of form I is given and differential characters of form II are discussed. A form of the disease has been observed in California which differs from the two forms in Michigan.

The histological effects of the disease are those common to other fusarial wilt diseases and besides vascular mycosis include a pronounced tracheal gummosis and tracheal bacteriosis in field plants.

The etiological relationship of Fusaria isolated from diseased plants has been proved by numerous infection experiments. Each isolate produces a single form of the disease, and its integrity has been constant in repeated passage through susceptible varieties of celery.

In classifying the pathogens the difficulties inherent to Fusarium taxonomy have been encountered and a critical discussion of current concepts of taxonomical criteria is presented. It is suggested that the host relationship has value equal to morphology for classifying parasitic members of section Elegans.

Methods for differentiating the form I and form II pathogens include color reactions on rice and responses to toxic substances in the culture medium. Only minor morphological differences were noted. The form I pathogen is made the type species, *Fusarium apii* n. sp., and the form II pathogen a variety of it, *F. apii* var. *pallidum*, n. var.

The effect of temperature on the pathogen, the relation of soil temperature and moisture to the growth of celery, and their effects on the disease were studied. The optimum temperature for growth of *F. apii* is 28-29° C. and for *F. apii* var. *pallidum* 26-28° C. Celery grew best at a soil temperature of 20° C., and the disease was most active at 26-30° C.

In the control of Fusarium yellows the exclusion of the pathogens from non-infested soils is recommended. Eradication experiments in 1914 and 1915 proved the ineffectiveness of chemical treatments of muck soils but demonstrated the effectiveness of steaming the soil. Certain cultural practices as palliative measures are recommended.

By breeding for resistance to Fusarium yellows varieties of celery have been produced that can be grown successfully on heavily infested soil. A resistant strain of Golden Self-Blanching was developed from a selection made in 1919. The Curly Leaf Easy-Blanching variety, a resistant green celery, was developed from a selection of Newark Market.

Michigan Golden, developed from the tall strain of Golden Self-Blanching, is highly resistant to Fusarium yellows and is a very desirable type. The results of field tests in 1933 and 1934 to compare the resistance of this strain with that of commercial yellow and green celeries are presented.

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